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UPPER JURASSIC
RHYNCHONELLID BRACHIOPODS
FROM NORTHWESTERN EUROPE

A. CHILDS

UPPER JURASSIC RHYNCHONELLID BRACHIOPODS FROM NORTHWESTERN EUROPE

BY

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SYNOPSIS

The major part of this study comprises a systematic revision of most of the Upper Jurassic rhynchonellids of northwestern Europe. Thirty-five species belonging to the genera *Monticarella*, *Lacunosella*, *Rhynchonella*, *Thurmannella*, *Acanthothiris*, *Acanthorhynchia*, *Somalirhynchia*, *Septaliphoria*, and *Torquirhynchia* gen. nov. are described. By using serial sectioning and acetate peel techniques, the internal structures of all but the rarest species have been investigated and the majority of these are described and figured for the first time. New taxa include six species, a subgenus, and a genus.

Observations on ecology and distribution are given with the specific descriptions and separate sections are also included dealing with these aspects at generic level.

INTRODUCTION

In contrast to the many monographs describing the complete faunas of small areas, this study consists of the examination of a single order, the Rhynchonellida, over a wider region; the author considering that this approach provides a much better basis for taxonomic as well as ecological and distributional studies. The rhynchonellid brachiopods are a morphologically diverse group and, although not numerous in the Upper Jurassic of the British Isles, they colonised a wide range of habitats in N.W. Europe during this period.

Although most of the species described have been previously figured, this is the first attempt to give such a comprehensive account of these faunas and to clarify their synonymies. It is interesting to note in this connection that the French literature abounds with Orbigny and Lamarck species, the German with those of Schlotheim, Oppel and Quenstedt while many British authors have relied on Sowerby and Davidson. By making a palaeontological study on a wider geographical basis than is usually attempted, it is hoped to reduce the number of species confined by national boundaries. It is considered that the other major justification for attempting to study a group over a relatively wide geographical area is that in considering evolutionary lineages this helps to eliminate any local distortion caused by migration and the general imperfection of the fossil record.

Although essentially work has been confined to taxa within the Upper Jurassic, certain species and genera from lower stratigraphical levels have been investigated where this was thought necessary. The type species of *Acanthorhynchia*, namely *A. panacanathina*, from the Bajocian has thus been included and similarly a study was made of *Acanthothiris spinosa* in order to determine the justification for splitting the spinose forms into separate genera.

Previous research

Although no previous author has attempted to produce such a comprehensive monograph of this group of rhynchonellids, there have been numerous descriptions and figures published over the last two hundred years. As there are relatively few rhynchonellids in the British Upper Jurassic rocks, most of the works referred to are by continental authors.

Linnaeus (1767) described only one of the species discussed below, namely *Acanthothiris spinosa*; this species was also the subject of the first figure to which reference is made, Knorr and Walch (1769). This appears to be the only recognisable eighteenth century description of a Middle or Upper Jurassic rhynchonellid. Of the workers of the early part of the nineteenth century, the most important were Schlotheim (1813, 1820), Zieten (1830–33) and, to a lesser extent, Lamarck (1819). The paucity of British Upper Jurassic material meant that the Sowerbys figured only one species—*Torquirhynchia inconstans*. Fischer de Waldheim's paper of 1809 must also be mentioned as this introduced the genus *Rhynchonella*. The major nineteenth century French work was undoubtedly d'Orbigny's (1850) "Prodrome", but this lost much of its potential value through lack of illustrations.

From about 1850 until the beginning of the present century several eminent palaeontologists produced many of the monographs still regarded as standard works. These writers included Davidson, who described and figured all the then known British brachiopods, Eudes-Deslongchamps, who produced numerous well illustrated papers on the brachiopod faunas of Normandy and elsewhere and Loriol and Haas who produced similar comprehensive works on the French and Swiss Jura. Many of the monographs of these authors set standards which have seldom been surpassed. Mention must also be made of the writings of Quenstedt (1851–52), which culminated in his magnificent work "Die Brachiopoden" (1868–71), still the most complete

illustrated account of European brachiopods. Apart from these, there are also numerous papers and monographs dealing with smaller areas such as those of Struckmann (1878) on the region of Hannover and Rothpletz (1886) on the Vilser Alps. The latter, while strictly outside the area under consideration, includes important discussion on the higher taxonomy of many of the species described.

UPPER JURASSIC ZONES AND STAGES	
nodiger	UPPER VOLGIAN
subditus	
fulgens	
giganteus	
gorei	
albani	
pallasiodes	
rotunda	
pectinatus	
wheatleyensis	
Subplanites spp.	LOWER VOLGIAN
Gravesia spp.	
pseudomutabilis	
mutabilis	
cymodoce	
baylei	KIMMERIDGIAN
pseudocordata	
transversarium	
cordatum	
mariae	OXFORDIAN

FIG. 1. The nomenclature of the Upper Jurassic zones and stages used in this study, following the recommendation of the British Mesozoic Committee as reported by Ager (1964).

During the present century there has been relatively little investigation of the Upper Jurassic rhynchonellids. Buckman (1918), as part of his "Burma Memoir", completely revised the taxonomy of the Jurassic rhynchonellids but this revision was largely based on Lower and Middle Jurassic British material and few of the species here described can be attributed to his genera. With regard to Buckman's work, Ager (1956) wrote, "His (Buckman's) classification is not now accepted, his terminology is unnecessarily complex and his emphasis in description is frequently misdirected". In 1917 Rollier produced his "Synopses" in which he attempted to elucidate the synonymies and redefine all Jurassic brachiopod species. While this work contains many useful suggestions, it was apparently undertaken without any reference to original specimens and consequently contains many misconceptions as a

result of referring to figures and descriptions which were inadequate in the first place. In 1920 Leidhold published a paper in which he proposed the genus *Septaliophoria* and two subgenera within it, namely *Thurmannella* and *Blochmannella*. Although the descriptions of the type species were inadequate, the names *Septaliophoria* and *Thurmannella* have since been widely used as a result of the lack of generic names at this level.

Probably the most notable contribution to the subject was Wiśniewska's (1932) monograph on the Upper Jurassic rhynchonellids of Poland. In that work she proposed the genera *Monticlarella*, *Lacunosella* and *Septocrurella* and in publishing the first transverse serial sections of many of the rhynchonellids of this age made a major advance in their study. The use of transverse serial sections was well known to several authors of the last century, notably Bittner and Rothpletz, but the technique was allowed to lapse until its use by Wiśniewska and its application was not widely publicised until Muir-Wood's paper in 1934. In common with virtually all the other works previously mentioned, Wiśniewska gave no details of lithology or associated fauna and very little information about relative abundance and distribution.

Since Wiśniewska, the only major work devoted to the Upper Jurassic brachiopods has been Makridin's (1964) study of the faunas of the Russian Platform. In this work Makridin was seriously handicapped by a lack of comparative material from the classic areas of N.W. Europe and, as a result, many of his assignations and conclusions are considered to be doubtful. Brief diagnoses of all the Mesozoic genera are to be found in Makridin (1960) and Ager (1965b). The ecological aspects of the Mesozoic brachiopod faunas have recently been discussed by Makridin (1964) and Ager (1965a).

II. ECOLOGY

The environments colonised by the rhynchonellids during the whole of the Mesozoic were discussed in detail by Ager (1965a). In that paper seven different habitats were recognized namely : (1) very shallow water sea floors, (2) sublittoral, sand grade sea floors without reefs, (3) sea floors in the vicinity of reefs, (4) shallow, non-depositional sea floors, (5) sublittoral, mud-grade sea floors, (6) deeper (?) bathyal mud-grade sea floors, (7) floating weed, and the adaptations shown by the Mesozoic brachiopods to each of them described. Within the area described by the present author, however, not all these environments appear to be present as the region was largely covered by a relatively shallow shelf sea. As far as they have been elucidated, the environments colonised by the rhynchonellids during the Upper Jurassic in northwestern Europe are as follows :

(a) Sandy, near-shore environments.

This facies is well developed in the lower and middle Oxfordian around the northern rim of the Paris Basin ; a similar environment was also present in much the same area during lower Callovian times and, while this is strictly outside the stratigraphical limits of this study, it is discussed for comparison. The formations representing this environment at these times were the "Terrain à Chailles" and

the "Varians Schichten" respectively. Both of them are sandy limestones, although they differ in that the former contains nodular layers of chert. Each of these formations contains an abundance of rhynchonellids and in each of them two markedly different types are present. The two rhynchonellids occurring in the "Terrain à Chailles" are *Septaliphoria arduennensis* (Oppel) and *Thurmannella obtrita* (Defrance). The former is much the larger and in having coarse ribs, a strong beak and a large pedicle opening was obviously adapted to a high energy environment. The much more abundant *T. obtrita* has relatively much finer ribbing and a very thin test, although it too has a well developed pedicle opening. Within the "Varians Schichten" the rhynchonellids are of much the same size and occur in similar proportions. In this case the larger is *Acanthothiris spinosa* (Linnaeus) and the smaller species is *Ivanoviella alemanica* (Rollier). The former, like *S. arduennensis*, tends to occur singly rather than the large groups in which *T. obtrita* and *Ivanoviella alemanica* are found. The latter species closely resembles *T. obtrita* externally except that it has stronger ribs and a more limited posterior smooth area. It is suggested that the similarity of environments in which *A. spinosa* and *S. arduennensis* are found, and the fact that the latter species is obviously adapted to living an attached existence in such conditions is strong evidence for regarding the spines of *A. spinosa* as an anchoring mechanism, especially as its pedicle atrophied during ontogeny. This view is in contrast to that of Rudwick (1965) who considered these spines to be of a sensory nature. It is thought that the smaller, thinner shelled *T. obtrita* and *I. alemanica* probably lived attached to algae. This idea is supported by the presence of the relatively large pedicle opening, while the very thin shell of *T. obtrita*, as seen in silicified material, would appear to preclude its survival on the bottom in such numbers in a high energy environment. However, it is always possible that they lived in sheltered niches within this environment.

The same type of environment is suggested for the deposition of the Lower Calcareous Grit as seen on the Yorkshire coast. In that area *Thurmannella* is again abundant but any larger rhynchonellids appear to be very much rarer although Mr. E. F. Owen (personal communication, 1966) states that he has found *Septaliphoria* on Filey Brigg. The material described below as *S. paucicosta* sp. nov. came from inland localities but it is not known whether or not the species is associated with *Thurmannella* sp. The amount of material in the B.M. (N.H.) would suggest that *S. paucicosta* is very common at least at its type locality of Hutton Bushel.

The nearest comparable lithology and environment in the Kimmeridgian is provided by the Alt-na-Cuile Sandstone of Sutherland. This latter formation is a decalcified sandstone containing a rich fauna of rhynchonellids preserved as casts. As far as can be determined, given the poor preservation, this seems to be a coarse ribbed form closely comparable with *Septaliphoria* but as its internal structures are not preserved its exact relationship cannot be determined. This latter species is described below under the name *Septaliphoria (?) septentrionalis* sp. nov. The Abbotsbury Ironstone (Kimmeridgian) of Dorset may also represent this type of environment. Here again, the fauna includes poorly preserved rhynchonellids doubtfully ascribed to *Septaliphoria (?) hudlestoni* (Rollier).

Ager (1965a) suggested that the strongly uniplicate rhynchonellids such as *Homoeorhynchia acuta* and *Rhynchonella loxiae* were characteristic of sand grade, sublittoral sea floors. However, it is not thought that all species of the genus *Rhynchonella* lived in this type of environment as at least two of them, namely, *R. subvariabilis* and *R. rivelensis*, occur in clays or marls. It appears from the relatively limited information available that the earlier species attributable to *Rhynchonella* s.s. are always found in such lithologies and that it is not until Volgian times that the genus is found in a more sandy facies which presumably represents a higher energy environment. Makridin (1964), who gives the range of *Rhynchonella* as late Kimmeridgian—early Cretaceous, states that, "members of the genus are most widespread in the shoaly facies of a sandy and sandy-clay sublittoral". If the above information is correct, then it is interesting to note that the genus became much more morphologically diverse on colonising the higher energy environment. It is possible that *Rhynchonella* only colonised these environments on the extinction of such genera as *Septaliphoria*. In order to account for the occurrence of *R. subvariabilis*, Ager suggested a pelagic mode of life and it is thought that such a mode of life would also best account for the occurrences of the earlier species of the genus such as *R. rivelensis* and *R. triplicosa*, this is discussed further below.

(b) *Sea floors in the vicinity of reefs.*

While Ager (1965a) referred exclusively to the forms encountered in the vicinity of hermatypic coral reefs, within the Upper Jurassic, it is possible to subdivide this environment according to whether the reefs are coral or sponge. The greatest development of sponge reefs is found in the regions of Swabia and Franconia where they flourished from middle Oxfordian to, at least, lower Volgian times. The rhynchonellid fauna associated with these reefs is very distinctive and consists almost entirely of species of the genus *Lacunosella*. The incidence of sponges with *Lacunosella* spp. is such as to suggest that the rhynchonellids were actually dependent on them. Middlemiss (1962) has recorded rhynchonellids within the folds of *Raphidonema* in the Lower Greensand at Faringdon, Berkshire, and this may possibly be a commensal relationship; unfortunately, details of the rhynchonellids were not given. It has also been suggested (Ager, 1965a) that *Orbirhynchia* of the Upper Cretaceous adopted a similar mode of life and it may be significant that both the latter genus and *Lacunosella* possess the distinctive blade-like falcifer crura. Apart from *Lacunosella*, the only other rhynchonellid genera known to occur in the sponge reef facies are *Acanthorhynchia* (*Echinirhynchia*) and *Monticarella*; these may well have been pelagic forms and are discussed further below.

The important factor in determining the distribution of the lacunosellids would seem to be the presence of sponges and whether these were living as reef assemblages, loose groups or "lenses" mattered little. While the greatest abundance and variety of lacunosellids is found in the sponge reefs of Germany where sponges were the dominant feature of the fauna during the Upper Jurassic, in the southern French Jura *L. arolica* occurs in calcareous shales with only isolated sponges.

The areas around the coral reefs appear to have been colonised by two genera. The more distinctive externally is *Torquirhynchia* gen. nov., which comprises a

series of strongly asymmetrical species, as typified by *T. inconstans* (J. Sowerby) from the Kimmeridge Clay. The reason for this somewhat bizarre development is not understood; however, it is interesting to note that the individuals concerned can be inverted and still retain the same form of anterior commissure. This is particularly obvious in the more globose specimens of *T. inconstans* in which the brachial valve was inflated to such an extent that the pedicle must have atrophied. Given the subspherical appearance of these inflated specimens, their lack of a pedicle and the fact that they apparently lived in a high energy, perireefal environment, it seems reasonable to assume that the development of asymmetry was related to these facts. That *Torquirhynchia* species can be inverted and still retain the same form of anterior commissure may possibly have been of advantage in that, as the right and left halves of the mantle cavity are physiologically independent (Orton, 1914), at least half of the lophophore system would have a water intake well clear of the bottom.

With the exception of *T. cf. T. astieriformis*, which was collected from around a small sponge reef, the genus has always been found associated either with corals or with "reef" limestones. *Torquirhynchia* seems to be completely absent from the sponge reef facies of the Swabian and Franconian Alb; *T. speciosa* is found in the Kelheim area but the "Dieras Kalk" in which it occurs has much closer affinities with the fauna of the Stramberk Limestone of Czechoslovakia.

Apart from *Torquirhynchia*, the only other genus to have colonised the areas around coral reefs is *Somalirhynchia* Weir. *S. moeschi* (Haas), which occurs widely in the central French Jura, is always associated with corals according to M. Enay (personal communication, 1965) and this was certainly so at the one locality where it was collected by the author. It is considered that the presence of corals in the Kimmeridgian Boulder Beds of Sutherland is significant in accounting for the occurrence of *S. sutherlandi*. This occurrence of *S. sutherlandi* is discussed in some detail under the specific description. It must be stressed that both *Torquirhynchia* and *Somalirhynchia* appear to be strictly perireefal. Elliot (1950) has suggested that the absence of brachiopods within reefs is probably a result of the coral polyps eating the brachiopod larvae.

(c) Sublittoral, muddy sea floors.

This is the remaining major environment in which rhynchonellids have been collected. As stated by Ager, it seems reasonable to assume that this is a deeper water facies than those discussed above, but this need not be so and the present writer would agree that the grain size of the substratum seems to be more important than the actual depth. With regard to this latter point, at various localities in the southern French Jura *Lacunosella arolica* occurs in a marly facies. However, as stated above, it is invariably associated with sponges and it is considered that these represented the substrate as far as the lacunostellids were concerned and consequently the presence of sponges is the determining factor rather than sediment or depth.

Other genera which occur in this environment include *Rhynchonella*, *Thurmannella*, *Echinirhynchia* and *Monticarella*. Of these it is suggested that forms such as *T.*

obtrita from the "Renggeri Marl" and *R. rivelensis* and *R. subvariabilis* from the upper Oxfordian and upper Kimmeridgian respectively were probably attached to algae during life. This is suggested as the normal mode of existence but does not preclude occasional specimens being drifted considerable distances and thus accounting for the occurrence of rare species such as *subvariabilis*, as suggested by Ager. *T. obtrita* and *R. rivelensis* occur in such abundance that it seems unlikely that they

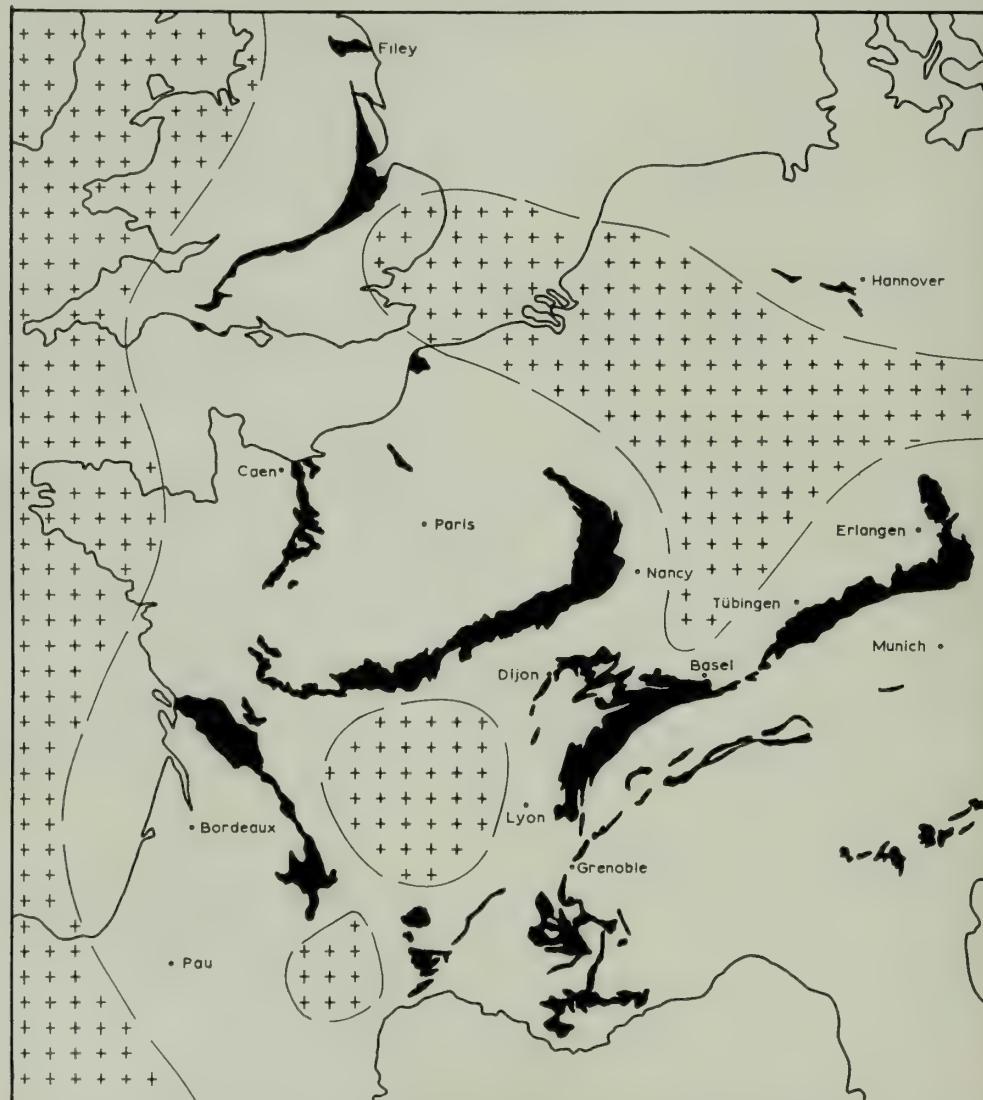


FIG. 2. The solid black area represents the outcrop of the Callovian-Volgian ; this information is taken from the map commissioned by the World Geological Congress of 1881. A generalized palaeogeography of the Oxfordian-Kimmeridgian (after Kuhn, 1953) is shown with the land areas ornamented with crosses.

are not in the area where they lived and this is borne out by the fact that ontogenetic series of *T. obtita* can be collected.

Concerning the remaining genus and subgenus, namely *Monticarella* and *Echinirhynchia*, the latter is known to occur in all the facies previously described apart from in association with corals while *Monticarella* is recorded from all except the near shore, high energy type. These observations, coupled with the small size of the

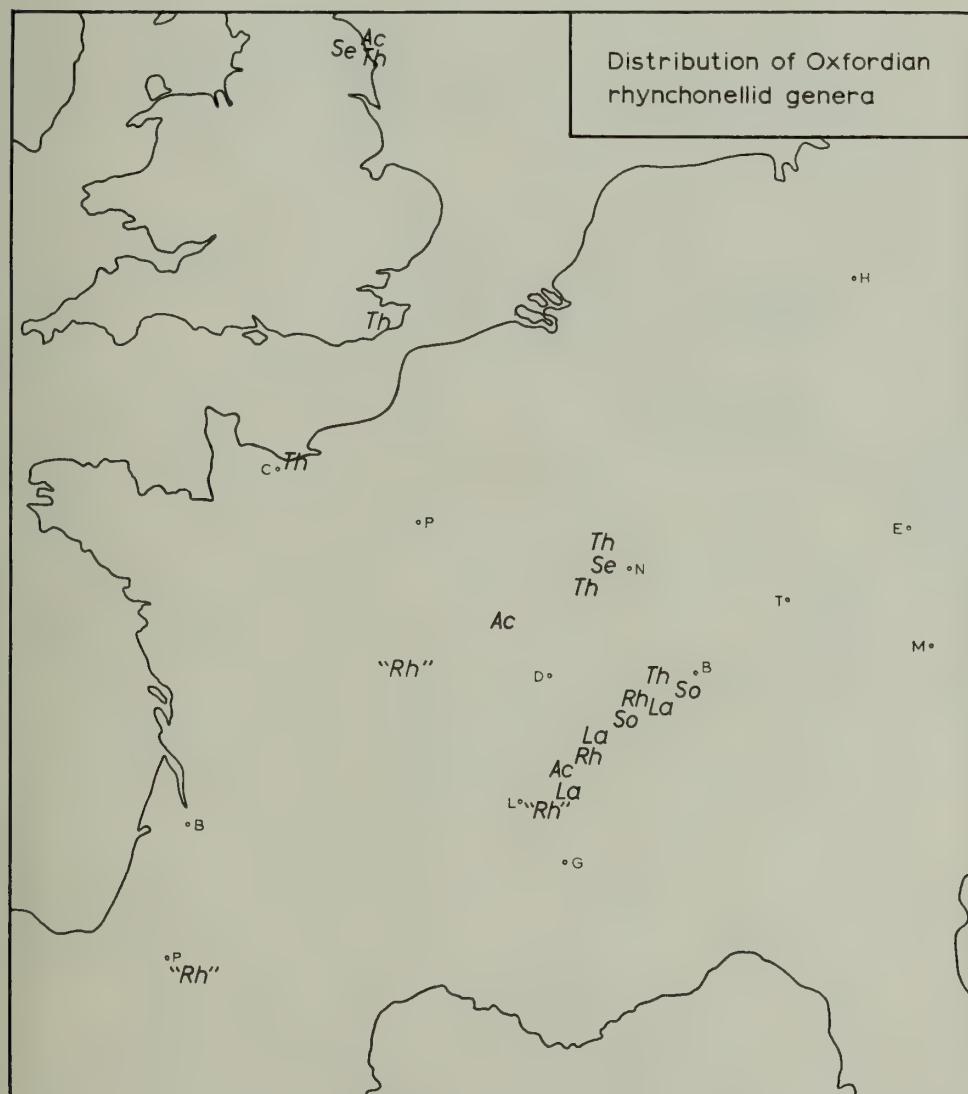


FIG. 3. Ac = *Acanthorhynchia*; La = *Lacunosella*; Rh = *Rhynchonella*; " Rh " = " *Rhynchonella* " ; Se = *Septaliphoria*; So = *Somalirhynchia*; Th = *Thurmannella*.

taxa concerned, suggest that they were attached to algae or sponges and consequently easily drifted long distances. While the normal mode of life may well have been the same as that of *Lacunosella*, the small size and delicate nature of the test obviously made it much easier for them to be transported over considerable distances and account for their appearance in such a diverse range of habitats.

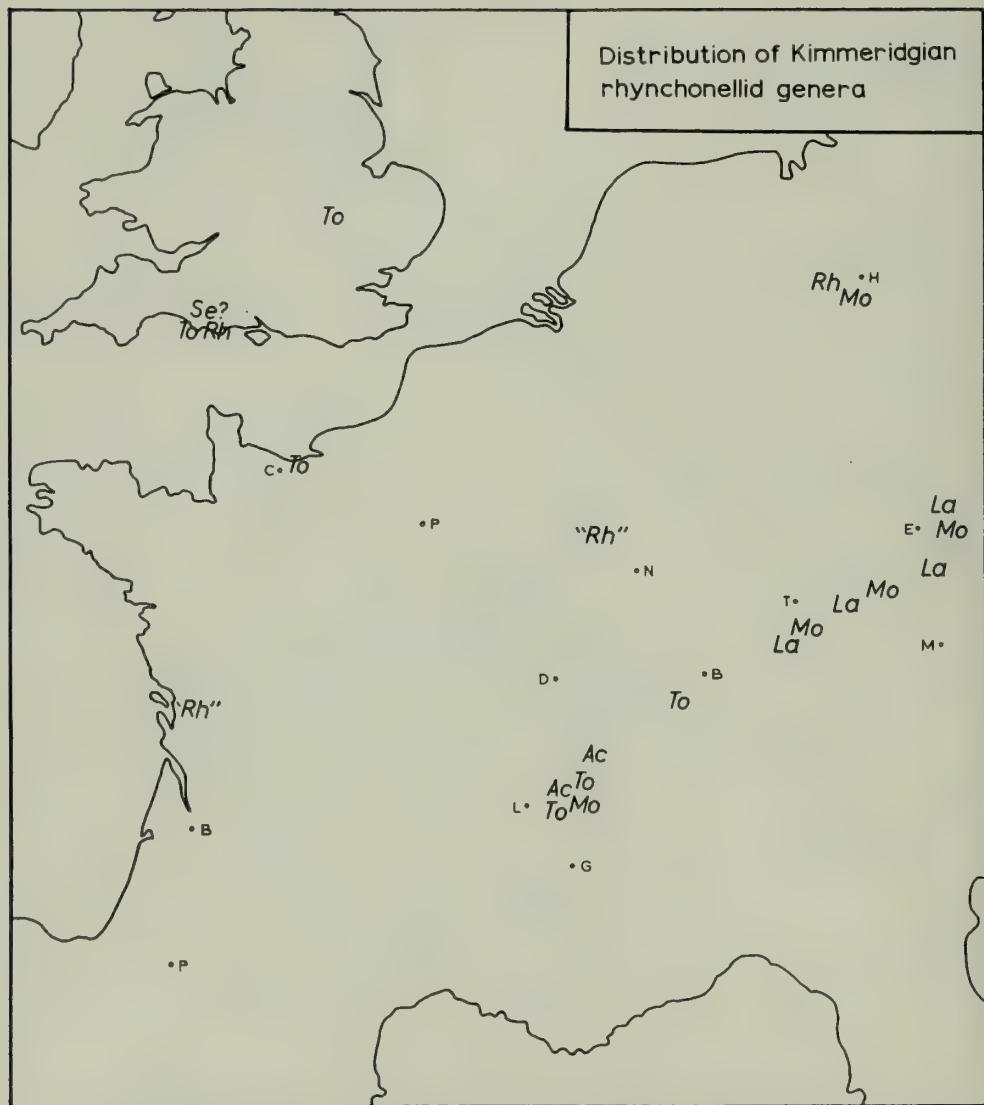


FIG. 4. Ac = *Acanthorhynchia*; La = *Lacunosella*; Mo = *Monticlarella*; Rh = *Rhynchonella*; "Rh" = "Rhynchonella"; Se? = *Septaliphoria*?; To = *Torquirhynchia*.

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION

Details of the distribution of individual species are given in the systematic part of this study but text-figs. 3-5 have been included to summarise the distribution of the genera. These figures are based on information obtained from field observations, museum collections and literature. It is considered that the distribution is largely controlled by facies and substrate, as shown by the occurrence of *Septaliphoria* and *Lacunosella*.

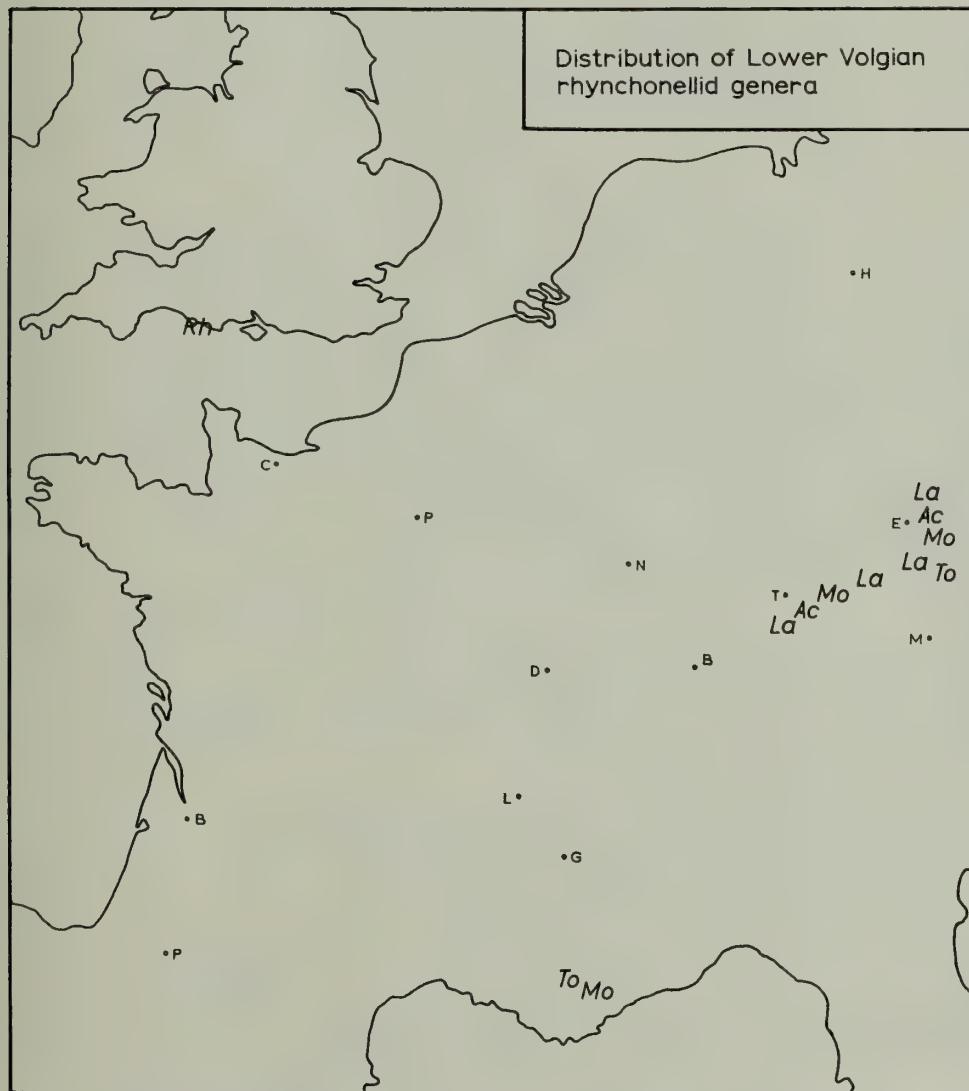


FIG. 5. Ac = *Acanthorhynchia*; La = *Lacunosella*; Mo = *Monticlarella*; Rh = *Rhynchonella*; To = *Torquirhynchia*.

JURASSIC RHYNCHONELLIDS

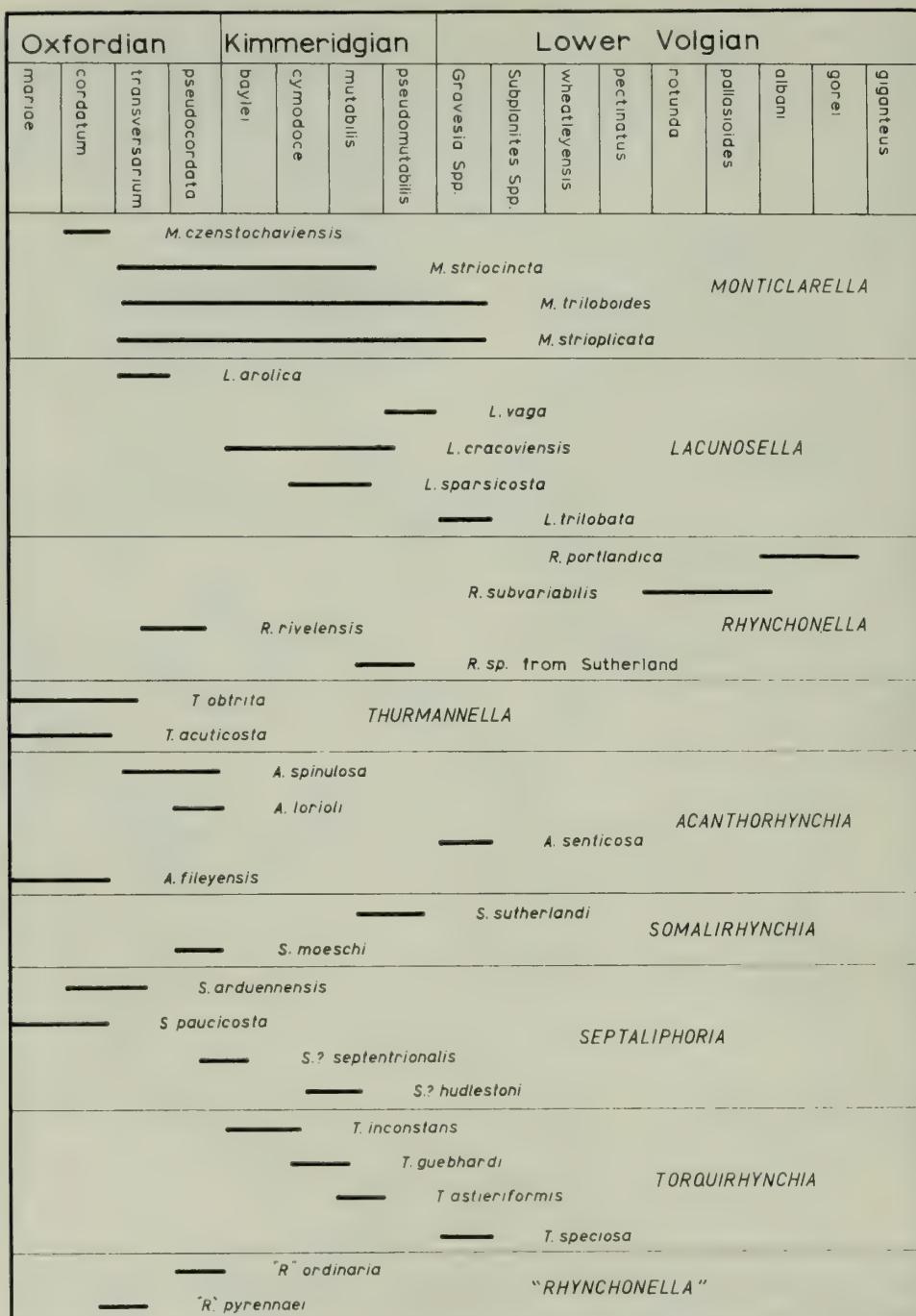


FIG. 6. The stratigraphical ranges of the Upper Jurassic rhynchonellids here described.

In order to help clarify the distribution patterns, text-fig. 2 shows the outcrop of the Upper Jurassic (including the Callovian) and also indicates a generalised palaeogeography of Oxfordian-Kimmeridgian times, after Kuhn (1953). Volgian times saw a major withdrawal of the sea from much of the area and the consequent marked decrease in the rhynchonellid faunas can be seen by comparing text-figs. 4 and 5. This decrease is particularly evident when it is considered that most of the German fauna plotted on text-fig. 5 is probably restricted to the *Gravesia* and *Subplanites* zones of the basal Volgian.

The stratigraphical ranges of the Oxfordian-Volgian species studied are tabulated on text-fig. 6. These ranges have been determined as accurately as possible, but it has often proved difficult to translate records from older stratigraphical papers into modern zonal terms.

MORPHOLOGY

The present author has accepted the definitions of morphological terms used in the "Treatise" (1965) with the exception of the following points :

Within the species studied, it has been found when describing the form of the pedicle opening the choice of term has invariably been limited to either hypothyridid or submesothyridid. In many cases it is extremely difficult to differentiate these types ; in none of the species examined did the pedicle opening strongly impinge on the beak ridges. The second point concerns the pedicle collar ; according to the definition in the "Treatise", this is an internal feature of the ventral beak, "continuous laterally with the internal surface of the deltidial plates". However, the feature figured by Thomson (1927) under that name consisted of a groove running from the posterior side of the pedicle opening to the tip of the beak. This latter structure has been found in the genus *Acanthothiris* and the term "pedicle trough" is proposed for it.

In describing the internal structures, care has been taken to stress when the features are being described as seen in transverse section and also to avoid misleading descriptions such as "septum long" when in fact it is high. The difficulties present in interpreting transverse sections are further discussed below with reference to the septalium.

The septalium has recently been defined in the "Treatise" as being a "Trough-like structure of the brachial valve between the hinge plates (or homologues), consisting of septalial plates (or homologues), enveloping and buttressed by median septum ; does not carry adductor muscles" ; the author would agree with this definition. However, it has been thought necessary to discuss this structure in some detail for two main reasons ; firstly, the author has collected silicified material of *Septaliphoria arduennensis* and *Thurmannella obtrita*, the species in which this structure was originally described by Leidhold (1920), and secondly, because there seems to be some confusion in the literature as to the appearance of the septalium as seen in transverse section.

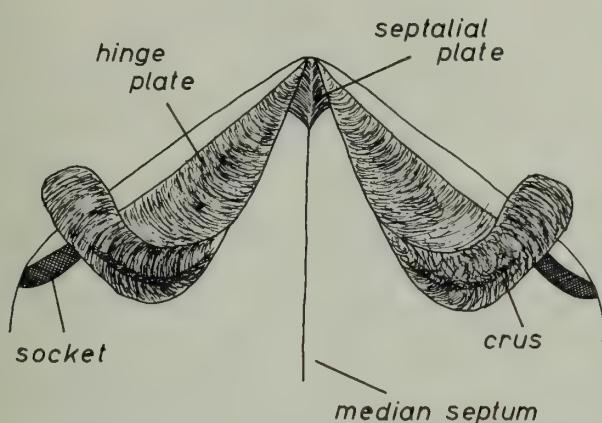
All the elements which together constitute the septalium are capable of considerable variation. This point would seem to be self-evident and yet has undoubtedly

been the cause of some of the misunderstanding. The first full description of the septalium showing its appearance in transverse section was given by Muir-Wood (1934) when she chose as her example the zeilleriid *Digonella digona* (Sowerby), despite the fact that it had originally been defined with reference to a rhynchonellid. The septalium found in *D. digona* is relatively shallow and supported by a high septum. These features, coupled with the flattened nature of the brachial valve, result in the appearance, in transverse section, of a septalium bearing little resemblance to the same structure as seen in most Mesozoic rhynchonellids. As stated above, the septalium in zeilleriids consists of a well developed, shallow trough lying between the hinge plates and supported for some distance by a high median septum. In contrast to this, the septalium in *Septaliphoria arduennensis* is only developed at the extreme posterior end of the valve and is either supported by a very low septum or, as pointed out by Wiśniewska (1932), sometimes appears to rest directly on the floor of the valve. The other point, which was recently discussed by Rousselle (1965), is that the appearance of the septalium in transverse section largely depends on the degree of inflation shown by the brachial valve.

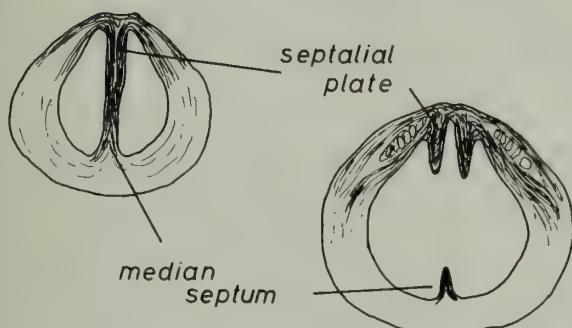
Text-figure 7 shows the septalium developed in *Septaliphoria arduennensis* and also two transverse sections through the posterior part of the brachial valve of *S. paucicosta* sp. nov. These demonstrate the way in which it is possible to have a septalium present and yet not to have the "diagnostic" U-shaped trough in the hinge plates developed in transverse section. From this it is evident that considerable thought should be given to the way in which shell globosity, angle of sectioning and relative development can cause the same structure to show considerable variation in appearance as seen in transverse section. Transverse sections of *S. paucicosta* rather than *S. arduennensis* have been illustrated as the fine detail was better preserved in that species. Rousselle (1965) suggested describing the septalium as either "apparent" or "non apparent" depending on whether or not it appeared "trough shaped" in transverse section. This suggestion does not seem to be particularly useful as a septalium is either present or it is not and its appearance in transverse section is obviously dependent on the factors mentioned above.

The transverse sections of *S. paucicosta* clearly show the way in which the septalial plates are united with the median septum. This latter point has been the subject of some discussion. The figured photomicrograph (pl. 12, fig. 6) of an acetate peel proves conclusively as has been pointed out by several authors (Ager, 1965b), that Leidhold (1920) was mistaken in describing the septalium as, "arising from a bifurcation of the dorsal septum at its posterior end and fusion of the forked structures with the hinge plate". The definition in the "Treatise", given above, is obviously the correct interpretation. A photomicrograph of a zeilleriid septalium is figured for comparison with that of *S. paucicosta* on pl. 12.

In the genera described, the author has recognized four of the crural types so far defined namely, radulifer, calcarifer, arcuifer and falcifer. The author would agree with the "Treatise" definitions with the exception of one point concerning the radulifer type. In the material studied, the radulifer crural bases do not arise on the ventral side of the hinge plates but on the dorsal. This is demonstrated by photo-



sketch of septalium as seen in silicified specimens of *Septaliphoria arduennensis* (Oppel).



transverse sections through posterior part of brachial valve of *S. paucicosta* sp.nov.

position of septalium (as seen in longitudinal section) in a rhynchonellid with an inflated brachial valve. (after Rousselle). with globose specimens the form of the septalium in transverse section is as figured above.

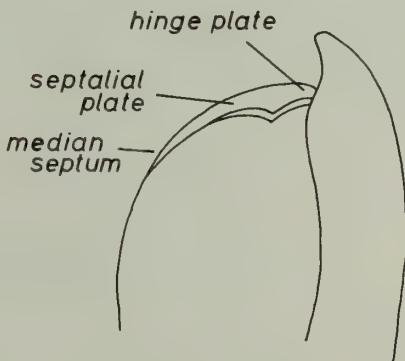


FIG. 7. Sketches to show the form of the septalium in the genus *Septaliphoria* Leidhold.

micrographs of an acetate peel of the crural bases of *Septaliphoria paucicosta* (pl. 12). In some species with radulifer crura such as *Acanthothiris spinosa*, the crural bases are only poorly differentiated.

Calcarifer type crura have been found in the genera *Thurmannella* and *Ivanoviella*; the form of the crura in these genera was strictly comparable to those observed in a specimen of *Rhynchonelloidella smithi* sectioned for comparison. Although, as pointed out in the "Treatise", distally the calcarifer are similar in form to the falcifer, in mode of occurrence and proximal appearance they differ markedly. Text-figures showing the form of falcifer crura are given with the specific descriptions of *Lacunosella arolica*, *L. sparsicosta*, *L. cracoviensis* and *L. vaga*. The most striking difference is that, by using acetate peels, it can be seen that the early formed parts of the crura lie within the hinge plates of the species with calcarifer crura while in *Lacunosella* the hinge plates are never united and the early formed parts of the crura are external to them and never surrounded by hingeplate material (pl. 12). This feature also differentiates falcifer crura from the radulifer and arcuifer types, apart from considerations of gross morphology. The crural bases are formed by the deflection of hinge plate material around these early formed portions of the crura (pl. 12). Whether or not the crural bases are clearly differentiated depends partly on whether the early crus was rounded or sharply pointed, and also on how closely the hinge plate material followed the original shape. Although the early crus may have been sharply pointed, this shape may be lost completely or reduced to a rounded swelling on the dorsal side of the hinge plates where the latter are much thickened.

Arcuifer crura are only recorded in the genus *Monticarella*. Three species of that genus were investigated, using acetate peels, but the preservation was poor in all cases and no information additional to that given in the "Treatise" was obtained.

Cardinal processes of the type found in certain Palaeozoic rhynchonellids such as the Uncinulidae are not developed in the material studied and, within the Upper Jurassic, only the genus *Acanthorhynchia* shows any comparable structure. In that genus the inner hinge plates are characteristically thickened and in some species this gives rise to a low rounded process on the ventral side of the hinge plates. A photomicrograph of the thickened hinge plates of *Acanthorhynchia* (*Acanthorhynchia*) *panacanathina* is figured on plate 12.

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHONELLACEA Gray, 1848

Family DIMERELLIDAE Buckman, 1918

Subfamily MONTICLARELLINAE nov.

DIAGNOSIS. Small rhynchonellids; ornament includes radial striae; ribs absent or variably developed; beak small and pointed; slightly sulcate, rectimarginate or weakly uniplicate; crura arcuifer where known.

STRATIGRAPHICAL RANGE. Lower Jurassic—basal Cenomanian.

Genus **MONTICLARELLA** Wiśniewska

- 1932 *Monticlarella* Wiśniewska, pp. 55-57.
 1960 *Monticlarella* Wiśniewska; Makridin, p. 248.
 1965b *Monticlarella* Wiśniewska; Ager, p. H604.

TYPE SPECIES. *Rhynchonella czenstochaviensis* Roemer, by original designation.

EMENDED DIAGNOSIS. Small subpentagonal or subtriangular rhynchonellids ; radial ornament always includes striae and usually ribs ; small, sharp beak; crura arcuifer.

STRATIGRAPHICAL RANGE. Upper Jurassic—? Lower Cretaceous.

DESCRIPTION. *External characters.* All the included species are small, subpentagonal or subtriangular, symmetrical and biconvex. The valves may be of equal convexity or the pedicle valve may be the more inflated. The small, pointed, suberect to erect beak does not obscure the hypothyridid pedicle opening ; deltoidal plates, when present, are small and disjunct. A small flattened interarea and distinct beak ridges are developed.

One of the most distinctive features is the ornament which always includes radial striae, even though these may be restricted to the troughs between the ribs. Ribs, rounded or subrounded, are usually present, although not on the type species : the variation in the development of the ribbing is a useful criterion for specific differentiation. The anterior commissure is either rectimarginate, uniplicate or slightly sulcate.

Internal characters. None of the specimens sectioned was particularly well preserved.

Pedicle valve. Dental lamellae are present but are usually only weakly developed and invariably only attached, if at all, to the extreme posterior of the valve. The teeth are strong and usually inserted almost vertically into their sockets.

Brachial valve. The median septum, if present, is low ; septalial plates are not developed. Inner and outer socket ridges are usually well differentiated.

The crura are of the type distinguished by Wiśniewska as arcuifer. She described them as having wide bases, being concave toward the middle and turning distally toward the ventral valve where they are terminated by "a sort of small crural plate in the shape of a hammer". The author would agree with Wiśniewska that the genus has a distinctive type of crura. The most distinctive feature about them as seen in transverse section would seem to be the way in which, from being initially flattened in the plane of articulation, by the development of vertical elements at their inner ends, they again become flattened but lying at right angles to the plane of articulation and slightly to the ventral side of it.

SPECIES. The following nominal species are attributed to the genus

- M. czenstochaviensis* (Roemer) (1870, p. 247, pl. xxii, figs. 12-14)
- M. lineolata* (Phillips) (as figured by Jacob and Fallot 1913, pp. 17-18, pl. i, figs. 9-14).
- M. rollieri* Wiśniewska (1931, pp. 59-60, pl. vi, figs. 10-11)
- M. striocincta* (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 24)
- M. strioplicata* (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 23)
- M. triloboides* (Quenstedt) (1852, p. 455, pl. xxxvi, fig. 29)

DISTRIBUTION. The genus occurs most commonly in the Swabian and Franconian Jura ; outside those areas it has only definitely been recorded from Poland and the French Jura and in both these regions it is a very scarce form. Makridin (1964) does not record it from the Russian Platform, although it is stated to occur there in the Russian " Treatise ".

OCCURRENCE. The three species investigated in detail all have consistently well developed pedicle openings which, it is reasonable to assume, indicate a functional pedicle in the adult stage. This latter fact, coupled with the wide distribution of the species and the fact that they can occur in a variety of high energy environments, suggests that the mode of life could well have been one of attachment either to sponges or floating material. This hypothesis would account for the diversity of environment in which the genus occurs.

***Monticlarella czenstochaviensis* (Roemer)**

(Pl. I, fig. 4, text-fig. 8)

1870 *Rhynchonella Czenstochaviensis* Roemer: 247-48, pl. 22, figs. 12-14.

1917 *Rhynchonella Czenstochaviensis* Roemer; Rollier: 116.

1932 *Monticlarella czenstochowiensis* (Roemer); Wiśniewska: 57-58, pl. 6, figs. 13-18.

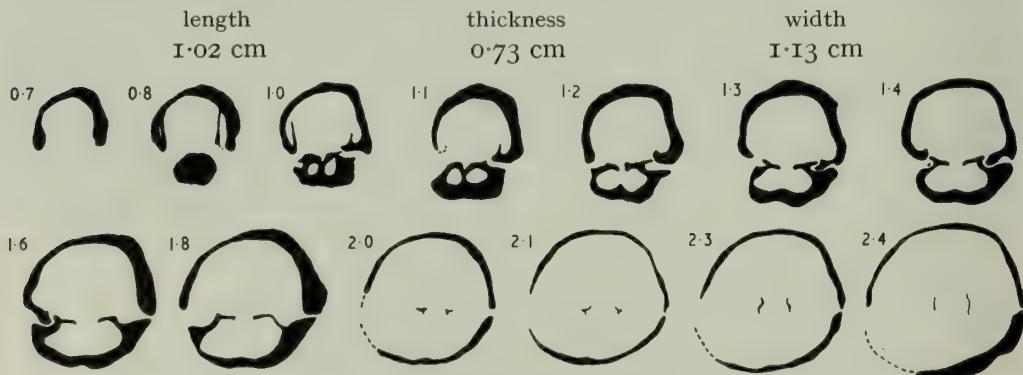
EMENDED DIAGNOSIS. Medium sized, subtriangular *Monticlarella* ; maximum width well toward anterior margin ; valves equally biconvex or with the pedicle valve the more inflated ; rectimarginate ; test covered by fine radial striae ; concentric growth lamellae may be present ; crura arcuifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*cordatum* zone.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Roemer (1870) pl. xxii, figs. 12-14, from " Clarenberges " near Czenstochowa, Poland.

MATERIAL. 5 specimens collected by Dr. D. A. B. Pearson from the Holy Cross Mts., Poland. 2 specimens obtained by Dr. D. V. Ager from the type locality.

DIMENSIONS OF FIGURED SPECIMEN.



***MONTICLARELLA CZENSTOCHOWIENSIS* (Roemer)**

Oxfordian, Poland. J.1219/2

FIG. 8. Transverse serial sections of *Monticlarella czenstochaviensis* (Roemer) kindly made available by Dr. D. V. Ager. Numerals represent distance in millimetres from pedicle umbo.

DISTRIBUTION. The species has only been recorded from Poland.

REMARKS. The figured specimen and the series of serial sections were kindly made available by Dr. D. V. Ager. Lack of material precludes a full description but, from the limited material available and the specimens which have been figured, the species appears to be both consistent and distinctive.

Although Wiśniewska (1932) did not give any reason why she changed the name, it is presumed that she did so on grounds of incorrect transliteration. However, as this is not permissible under the International Code of Zoological Nomenclature, Article 32, (a) ii, the author has reverted to the original spelling of Roemer (1870).

***Monticlarella striocincta* (Quenstedt)**

(Pl. I, figs. 1-3, text-fig. 9)

- 1852 *Terebratula striocincta* Quenstedt: 455, pl. 26, fig. 24.
- 1858 *Terebratula striocincta* Quenstedt: 634, pl. 78, fig. 12.
- 1871 *Terebratula striocincta* Quenstedt: 131, pl. 40, figs. 17-19.
- 1885 *Terebratula striocincta* Quenstedt: 694, pl. 53, fig. 57.
- 1886 *Rhynchonella cf. striocincta* (Quenstedt); Oppel and Waagen: 295.
- 1917 *Rhynchonella striocincta* (Quenstedt); Rollier: 119.
- 1932 *Monticlarella striocincta* (Quenstedt); Wiśniewska: 58-59, pl. 6, fig. 12.

EMENDED DIAGNOSIS. Small, subpentagonal *Monticlarella*; anterior commissure rectimarginate or slightly sulcate; pedicle valve much more inflated than the brachial; ornament of fine striae passing anteriorly into coarser ribs; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian: *transversarium* to *mutabilis* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 16, pl. 40 in Quenstedt (1871) from the "Malm gamma" of Lochen, Germany.

MATERIAL. 90 specimens from the collection of the University of Tübingen; 2 specimens collected by the author from the southern French Jura; 1 specimen from the collection of the Geology Department, Imperial College, London.

DESCRIPTION. *External characters.* The shell is biconvex with the pedicle valve the more inflated; this results largely from the distinctive manner in which the posterior part of the pedicle valve bends over so that the top of the very small, pointed beak lies almost at right angles to the lateral commissure. Although the beak lies in this position it is not sufficiently incurved to obscure the delthyrium. In the material studied, the small, disjunct deltidial plates mentioned by Wiśniewska (1932) have not been observed and there is an open delthyrium.

The test ornament is distinctive and consists posteriorly of numerous fine striae which pass anteriorly into well developed, rounded ribs formed by the fusion of several striae; the striae continue in the troughs between the ribs as far as the anterior margin. Growth lamellae are usually present but tend to be sparsely distributed and only poorly developed.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
0·80 cm	0·55 cm	0·75 cm
0·92 cm	0·67 cm	0·83 cm
0·88 cm	0·60 cm	0·86 cm

Internal characters. *Pedicle valve.* The dental lamellae are very much reduced and not attached to the ventral wall of the shell. The teeth are inserted at a relatively shallow angle, as seen in transverse section.

Brachial valve. There is no median septum. The sockets are shallow and inner and outer socket ridges are scarcely differentiated.

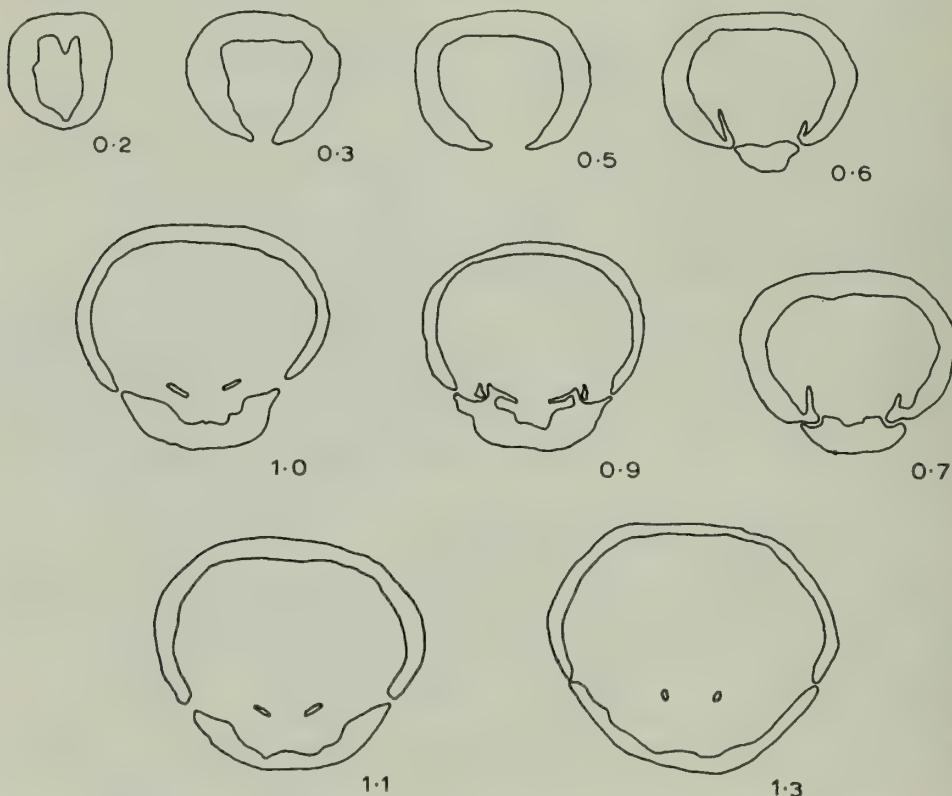


FIG. 9. Transverse serial sections of *Monticlarella striocincta* (Quenstedt). "Weiss Jura alpha". Lochengründle, Germany. Specimen donated by the University of Tübingen. ($\times 8$).

DISTRIBUTION. The Swabian and Franconian Jura, Poland and the southern French Jura are the only areas from which the species has been definitely recorded. It is considered likely that *M. striocincta* could occur quite widely in the French Jura but has been overlooked on account of its small size.

OCCURRENCE. Unfortunately Wiśniewska (1932) does not give any details of the associated fauna or of the type of lithology from which her material was obtained and Quenstedt (1852, 1871) only says that it occurs with *Terebratula lacunosa*. However, the author visited the original Quenstedt locality of Lochengründle near Tübingen and collected material from "Malm upper alpha" and "lower beta". Both of these horizons are within the sponge reef facies and consist there of interbedded hard, argillaceous limestones and marls, occurring in units ranging from a few inches to two or three feet in thickness. *M. striocincta*, together with *M. strioplicata*, was found to occur predominantly in the marly units and was associated with a varied fauna of terebratulids, including the ribbed "*pectunculus*" types, echinoid plates and spines, small ammonites and sponges; lacunosellid brachiopods were present but were concentrated in the harder limestone bands.

In the southern French Jura (Ain), the species has been collected from the Bedded Virieu Limestone (Ager & Evamy, 1963) just north of Lac d'Armaille. The Bedded Virieu Limestone is here represented by well bedded calc-lutites with alternations of calcareous shale; as well as *M. striocincta*, there is a rich fauna of lamellibranchs, terebratulids and the large asymmetrical rhynchonellid *Torquirhynchia guebhardi*. *M. striocincta* is one of the least abundant elements of the fauna, the majority of which suggests a high energy environment at or above wave-base (Evamy, 1963 unpublished thesis). *M. striocincta* has also been collected in this area from the argillaceous Chavoley Beds and details of the occurrence are given under *Lacunosella arolica*.

Monticarella triloboides (Quenstedt)

(Pl. I, figs. 5-7, text-fig. 10)

- 1852 *Terebratula triloboides* Quenstedt: 455, pl. 26, fig. 29.
- 1858 *Terebratula triloboides* Quenstedt: 643, pl. 78, fig. 13.
- 1871 *Terebratula triloboides* Quenstedt: 129, pl. 40, figs. 6-9.
- 1876 *Rhynchonella triloboides* (Quenstedt); Loriol: 188, pl. 23, figs. 41-43.
- 1885 *Terebratula triloboides* Quenstedt: 694, pl. 53, fig. 58.
- 1904 *Rhynchonella triloboides* (Quenstedt); Loriol: 279, pl. 27, figs. 36-38.
- 1913 *Rhynchonella triloboides* (Quenstedt); Jacob and Fallot: 34.
- 1917 *Rhynchonella triloboides* (Quenstedt); Rollier: 119.
- 1918 *Stolmorhynchia triloboides* (Quenstedt); Buckman: 46.
- 1932 *Monticarella triloboides* (Quenstedt); Wiśniewska: 62-63, pl. 6, figs. 8-9.

EMENDED DIAGNOSIS. Medium to large sized subpentagonal *Monticarella*; about 15-20 simple ribs; no posterior smooth area; radial striae only present in the troughs between the ribs; uniplication in anterior commissure; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; accurate records range from the *transversarium* to *Gravesia* zones, Quenstedt states that it is most abundant in the "Malm gamma", i.e. *cymodoce* and *mutabilis* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 8, pl. 40 of Quenstedt (1871) from the "Malm gamma" of Bosler, Germany.

MATERIAL. 320 specimens from the collection of the University of Tübingen; 17 specimens collected by Dr. Enay from near Arinthod (Jura).

DESCRIPTION. *External characters.* The shell is equally biconvex and has a small, pointed, erect beak. The oval pedicle foramen is flanked by disjunct deltidial plates which show a characteristic thickening around the actual opening. Beak ridges and interarea are both well developed.

The ornament consists of about 20 rounded ribs, as counted at the anterior margin, which mostly originate at the umbones although a few also arise by dichotomy. The well marked uniplication in the anterior commissure usually carries about six of these ribs. A distinctive feature of the species is the radial striae which can be seen only in the troughs between the ribs of well preserved specimens; these striae are usually most easily observable toward the anterior margin. The better preserved specimens also show a concentric ornament of very fine growth lines, which are usually more apparent posteriorly; growth lamellae are rarely developed.

The shell of many of the broken and worn specimens is seen to be of a very fibrous character; whether this is its original condition or the result of post-burial recrystallisation, as evidenced by the loss of the fine detail, is not known. Although the shell fibres and the radial striae superficially resemble one another, the striae may be differentiated by the fact that they are more individually distinct and occur only in the troughs, whereas the fibres appear as a compact mass and may be visible on any part of the shell. If the top layer of the shell has been removed so that the fibrous condition is visible, this inevitably means that the striae will have been obliterated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·00 cm	0·68 cm	1·00 cm
0·87 cm	0·59 cm	0·87 cm
1·27 cm	0·84 cm	1·26 cm

Internal characters. Pedicle valve. The shell is quite thick and the dental lamellae are relatively well developed. The teeth are inserted vertically into the sockets, as seen in transverse section.

Brachial valve. There is no median septum or ridge developed; other details are as in generic description.

DISTRIBUTION. The species is known from the Swabian and Franconian Jura, Poland and the central French Jura. The only other record is that of Jacob and Fallot (1913) from the "Portlandien supérieur" of Chomérac (Ardèche).

OCCURRENCE. The author has not collected the species and it is only briefly recorded in the literature. Quenstedt (1871) noted that it occurred with *Terebratula lacunosa*. The horizon cited by Jacob and Fallot appears to yield a very varied rhynchonellid fauna, some of which is almost certainly referable to the genus *Lacunosella* Wiśniewska. The material of Dr. Enay came from a fine grained marl from which specimens of *Acanthorhynchia* (*Echinirhynchia*) *lorioli* were also obtained.

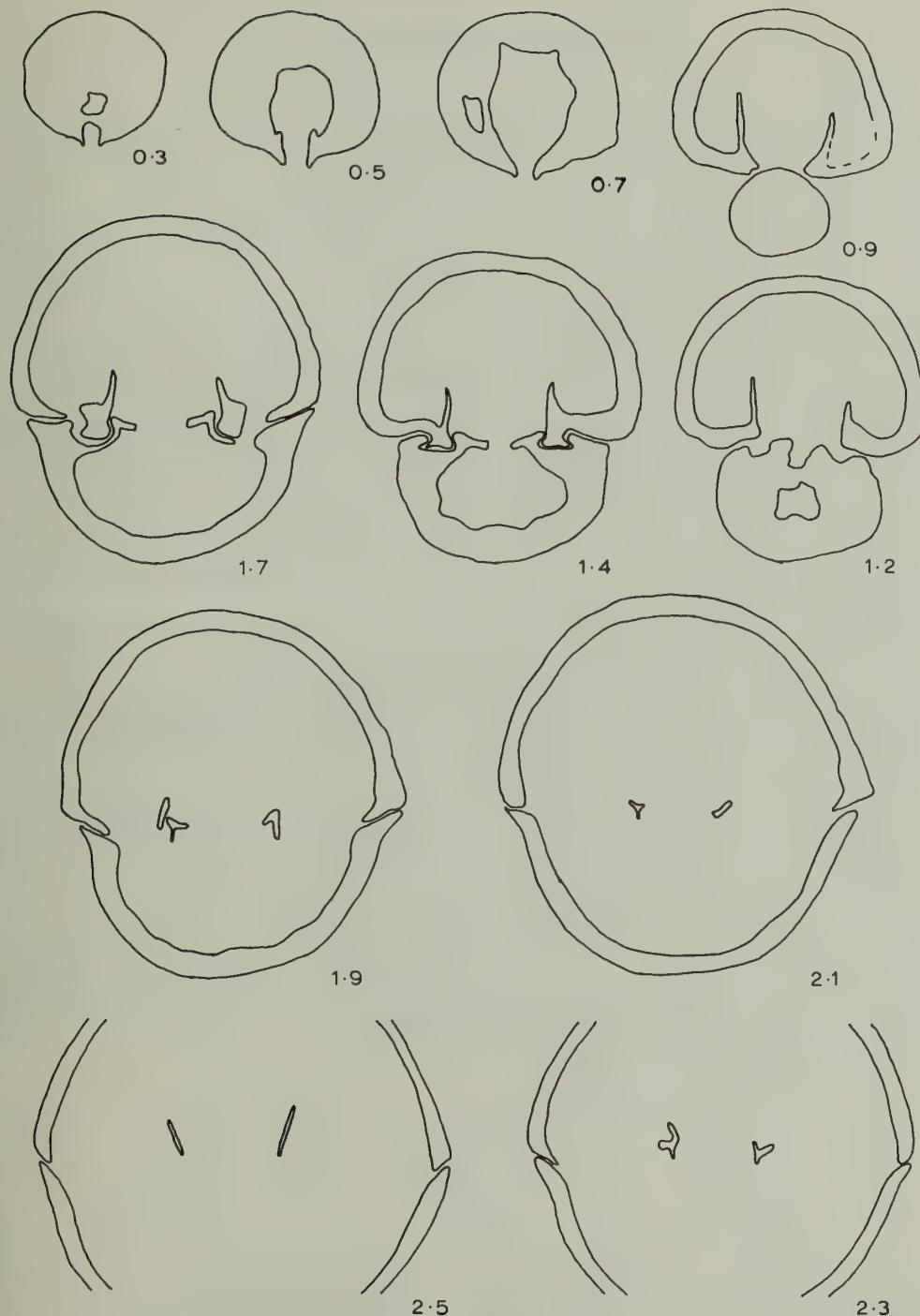


FIG. 10. Transverse serial sections of *Monticlarella triloboides* (Quenstedt). "Malm gamma", Germany. Specimen donated by the University of Tübingen. ($\times 8$).

Monticlarella strioplicata (Quenstedt)

(Pl. I, figs. 8-10, text-fig. II)

- 1852 *Terebratula strioplicata* Quenstedt: 455, pl. 26, fig. 23.
 1858 *Terebratula strioplicata* Quenstedt: 635, pl. 78, fig. 24.
 1871 *Terebratula strioplicata* Quenstedt: 132, pl. 40, figs. 24-32.
 1885 *Terebratula strioplicata* Quenstedt: 694, pl. 53, fig. 59.
 1909 *Rhynchonella strioplicata* (Quenstedt); Simionescu: 40, 41, 94, pl. 7, fig. 18.
 1913 *Rhynchonella strioplicata* (Quenstedt); Jacob and Fallot: 17.
 1917 *Rhynchonella strioplicata* (Quenstedt); Rollier: 123.
 1917 *Rhynchonella strioplanata* (Quenstedt); Rollier: 123.
 1917 *Rhynchonella pauciplicata* Rollier: 123.
 1917 *Rhynchonella tenuiplicata* Rollier: 123.
 1917 *Rhynchonella furcatella* Rollier: 123.
 1932 *Monticlarella strioplicata* (Quenstedt); Wiśniewska: 60-62, pl. 6, figs. 1-7, text-fig. 18.

EMENDED DIAGNOSIS. Medium sized, subpentagonal to slightly elongate *Monticlarella*; rectimarginate or with a low uniplication; ornament of fine striae posteriorly passing anteriorly into short coarse ribs; crura arcuifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; *transversarium* to *Gravesia* zones.

TYPE SPECIMEN. Lectotype, here designated, fig. 25, pl. 40 of Quenstedt (1871) from the "Malm gamma" of Lochen, Germany.

MATERIAL. 11 specimens from the collection of the University of Tübingen; 22 collected by the author from Swabia and Franconia.

DESCRIPTION. *External characters.* The shell is biconvex with the pedicle valve slightly more inflated than the brachial. The beak is small, sharply pointed and erect. The oval, hypothyridid pedicle opening is small and is flanked by two small, discrete deltidial plates. Beak ridges and interarea are only poorly developed.

Posteriorly the ornament consists of very fine striae, while on the anterior half or third of the shell are developed five or six relatively coarse ribs. The fine striae continue to the anterior of the shell only in the troughs between the ribs. The outline varies from subpentagonal to suboval, specimens having the former shape being wider and having more ribs; the length is usually greater than the width. There appears to be a complete gradation between the two forms at all stratigraphical levels for which there is material available; however, the material is relatively limited and it is not possible to say whether the proportions of the two forms change or have any stratigraphical value.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.18 cm	0.80 cm	1.13 cm
1.04 cm	0.68 cm	0.98 cm
1.05 cm	0.70 cm	0.78 cm

Internal characters. Pedicle valve. Dental lamellae are present but only poorly developed and attached to the shell wall only at their posterior extremities. The teeth are strong.

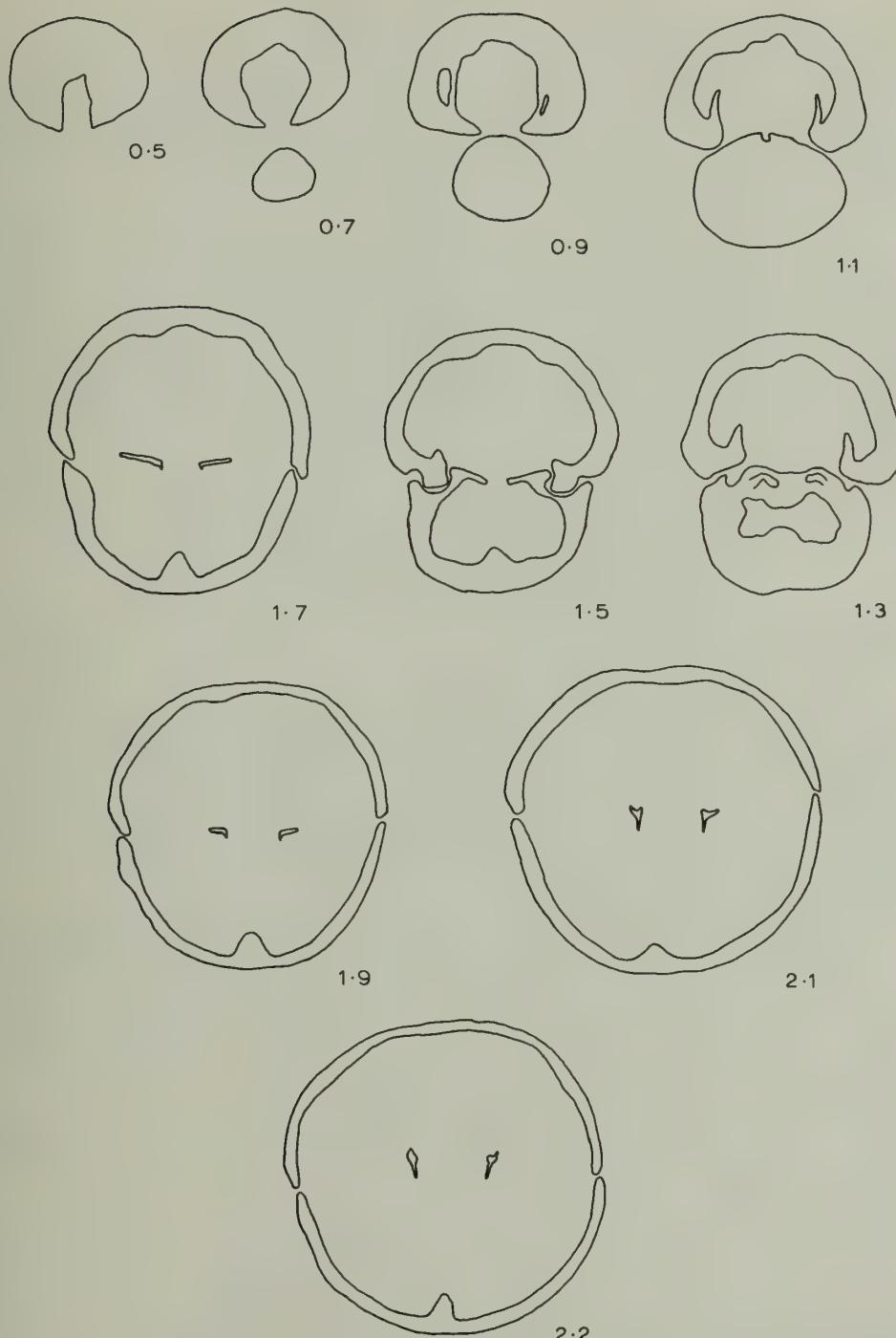


FIG. 11. Transverse serial sections of *Monticlarella strioplicata* (Quenstedt). "Malm gamma". Barrenberg, Germany. ($\times 8$).

Brachial valve. A long, well developed median ridge is present. The hinge plates are flat. Both the inner and outer socket ridges are clearly differentiated.

DISTRIBUTION. Apart from the Swabian and Franconian Jura and Poland, the only other records of the species are those of Jacob and Fallot (1913) from Mont Crussol and from Chomérac (Ardèche). A possible specimen of *M. strioplicata* was figured by Struckman (1878) from near Hanover.

OCCURRENCE. The species has been collected by the author from only two localities, namely, at Lochengründle in the Swabian Jura and at Barrenberg in Franconia. The former locality has been described in the remarks on the occurrence of *M. striocincta*. The latter locality is of "Malm gamma" age and is again in the sponge reef facies. The fauna included many lacunosellids, terebratulids, small sponges, ammonites and occasional belemnites and echinoids, with *M. strioplicata* one of the least abundant faunal elements. This locality is further described under *Lacunosella sparsicosta*.

Family WELLERELLIDAE Likarev in Rzhonsnitskaya, 1956

Subfamily LACUNOSELLINAE Smirnova, 1963

Genus **LACUNOSELLA** Wiśniewska, 1932

- 1932 *Lacunosella* Wiśniewska: 30–32.
- 1960 *Lacunosella* Wiśniewska; Makridin: 254.
- 1965 *Lacunosella* Wiśniewska; Ager: 608.

TYPE SPECIES. *Rhynchonella arolica* Oppel, by original designation.

EMENDED DIAGNOSIS. Medium to large rhynchonellids; outline usually subpentagonal; ribs bifurcate; beak small; beak ridges and interarea poorly developed; shell massive; very reduced dental lamellae; crura falcifer.

STRATIGRAPHICAL RANGE. Oxfordian—Kimmeridgian—Lower Volgian; upper *cordatum* to *Gravesia* spp. zones.

DESCRIPTION. *External characters.* The shell is either equally biconvex or with the brachial valve the more inflated. The test frequently has a characteristic and distinctive translucent, pearly appearance. Although the outline is usually subpentagonal, it may be strongly trilobate as in *L. trilobata*. The genus is usually symmetrically developed with a uniplication in the anterior commissure, however, this feature is frequently displaced by asymmetrical development and completely asymmetrical, bilobed variants are produced by *L. trilobata*.

The ribbing is variable and in different species the rib count at the anterior commissure varies between five and twenty-five. One of the most distinctive external features is that while not all the ribs bifurcate, this character is invariably shown by some of them.

A small suberect beak is present, as are beak ridges and an interarea although both the latter are only poorly developed. The submesothyridid pedicle opening is flanked by conjunct deltoidal plates. Concentric ornament, which is neither strongly developed nor consistently present, comprises fine growth lines and weakly developed growth lamellae.

Internal characters. *Pedicle valve.* The most striking features are the massive shell and the very reduced dental lamellae ; lateral cavities are hardly developed. Pedicle collars were not present in all the species sectioned but as it seems probable that these are only developed in the adult specimens, their absence may be the result of sectioning slightly immature material. The teeth are strong and frequently show some degree of crenulation ; lateral denticulae are usually present. In fully adult specimens the muscle attachment areas can be clearly seen as quite deep depressions in the shell.

Brachial valve. There is no septalium and the median septum, if present, is very much reduced. The hinge plates are divided and, almost as soon as the cavity of the brachial valve is exposed during serial sectioning, the long falcifer crura can be seen hanging down from them into the brachial valve. The presence of falcifer crura distinguishes *Lacunosella* from all other Upper Jurassic genera. Inner and outer socket ridges are both well-developed.

SPECIES. The following nominal species are attributed to the genus :

- L. amstettensis* (Fraas) (1858, pp. 107-8)
- L. arolica* (Oppel) (1865, p. 312)
- L. blanowicensis* Wiśniewska (1932, pp. 40-1, pl. iii, figs. 1-5)
- L. cracoviensis* (Quenstedt) (1871, p. 136, pl. xl, fig. 43)
- L. dilatata* (Rollier) (1917, p. 134)
- L. kozlowskii* Wiśniewska, (1932, pp. 54-55, pl. v, figs. 1-7)
- L. monsalvensis* (Gilliéron) (1873, p. 244, pl. x, figs. 11-12)
- L. multiplicata* (Zieten) (1832, p. 55, pl. xli, fig. 5)
- L. polita* (Quenstedt) (1871, p. 126, pl. xxxix, fig. 106)
- L. prosimilis* (Rollier) (1917, p. 174)
- L. pseudodecorata* (Rollier) (1917, p. 139)
- L. selliformis* (Lewiński) (1908, p. 437, pl. xxii, fig. 8-11)
- L. silicea* (Quenstedt) (1871, p. 129, pl. xxxix, fig. 107)
- L. siemiradzkii* (Wiśniewska) (1932, pp. 48-49, pl. iii, figs. 21, 22)
- L. sparsicosta* (Quenstedt) (1858, pp. 633-34, pl. lxxviii, figs. 12-22)
- L. subsimilis* (Schlotheim) (1820, p. 264)
- L. trilobata* (Zieten) (1832, p. 56, pl. xlvi, fig. 3)
- L. trilobataeformis* Wiśniewska (1932, pp. 46-48, pl. iv, figs. 1-11)
- L. vaga* sp. nov.
- L. visulica* (Oppel) (1866, p. 295).

DISTRIBUTION. The genus has been recorded throughout the French, German and Swiss Jura, from Poland and from Stramberk, Czechoslovakia.

OCCURRENCE. With the exception of the occurrence of *L. vaga* on the Col du Chat (Savoie) the genus is always associated with sponges. This association has been commented on by Quenstedt (1871), Ager and Evamy (1963) and Ager (1965a). The genus is most abundant and varied in the Swabian and Franconian Jura where it occurs in the bedded limestones associated with the sponge reefs.

The massive shell and consistent presence of a pedicle opening, presumably indicating a functional pedicle, seem to be adaptations to a high energy environment

around the reefs. The persistent occurrence of sponges with *Lacunosella* is so striking that it suggests that the genus was in some way dependent on them. Several times while collecting material, the author found specimens of *Lacunosella* actually in contact with sponges. While this may have been coincidence, it could also have been the result of the rhynchonellids actually having been attached to the sponges. It is difficult to see what particular benefit this would have been and why *Lacunosella* should have restricted itself to attachment on that particular 'host'. At the locality mentioned above where sponges are not present, *L. vaga* was obtained from bedded limestones associated with "reef" limestones.

***Lacunosella arolica* (Oppel)**
(Pl. I, figs. 11-12, text-figs. 12-13)

- 1864 *Rhynchonella lacunosa* (Schlotheim); Heer: 137, fig. 87.
- 1865 *Rhynchonella Arolica* Oppel: 312.
- 1866 *Rhynchonella Arolica* Oppel; Oppel and Waagen: 294.
- 1867 *Rhynchonella Arolica* Oppel; Moesch: 310-311, pl. 7, fig. 9.
- 1871 *Terebratula lacunosa Arolica* Quenstedt: 127, pl. 39, figs. 95-96.
- 1885 *Terebratula lacunosa Arolica* Quenstedt: 693, pl. 53, fig. 60.
- 1890 *Rhynchonella lacunosa* (Quenstedt) var. *Arolica* Oppel; Haas: 48-50, pl. 3, figs. 1-22, pl. 4, figs. 1-5.
- 1917 *Rhynchonella Arolica* Oppel; Rollier: 134.
- 1918 *Stolmorrhynchia arolica* (Oppel); Buckman: 46.
- 1932 *Lacunosella arolica* (Oppel); Wiśniewska: 33-38, pl. 2, figs. 1-18.

EMENDED DIAGNOSIS. Medium to large sized, relatively flattened *Lacunosella*; outline subpentagonal; 9-11 low, subangular ribs; crura falcifer.

STRATIGRAPHICAL RANGE. Oxfordian—upper *cordatum* and *transversarium* zones.

TYPE SPECIMEN. In his original description of the species Oppel cited the figure in Heer (1864) listed above.

MATERIAL. 16 specimens collected by the author from the southern French Jura in the British Museum (Nat. Hist.) nos. BB. 45630-45639, BB. 45678-45681; 43 specimens collected by Dr. Enay from the central French Jura; 12 specimens from the "Birmensdorfer-Schichten" of Switzerland donated by the Naturhistorisches Museum, Basel.

DESCRIPTION. *External characters.* The shell is biconvex with the brachial valve slightly the more inflated; however, both valves are relatively flattened compared with other species of the genus. The beak is small and suberect; beak ridges and interarea are hardly differentiated. The small, submesothyridid pedicle opening is flanked by conjunct deltoidal plates.

The radial ornament consists of about eleven low, subangular ribs, the majority of which originate at the umbones although bifurcation is not uncommon. Numerous fine growth lamellae are characteristically present. The anterior commissure has a well-marked uniplication which usually carries three or four ribs; however, it is often distorted to some degree by asymmetrical development.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·30 cm	2·35 cm	3·78 cm
2·86 cm	2·20 cm	3·22 cm

Internal characters. The internal characters have been investigated using material collected near Virieu-le-Grand (Ain) in the southern French Jura. Although not topotypic, the material is of the correct age and is not far from Trept (Isère), a locality mentioned by Oppel (1866) in his original description of the species.

Pedicle valve. A well developed pedicle collar is present in adult specimens. The shell is massive and while lateral cavities are present they are of a very reduced nature and bounded by slender dental lamellae. Although the dental lamellae are very slight, the teeth are strongly supported by the thick shell wall.

Brachial valve. There is a low median septum; other characters as in generic description.

DISTRIBUTION. The species appears to occur quite abundantly throughout the French and Swiss Jura and in Poland. That *L. arolica* has not been recorded from either the Swabian or Franconian Jura is attributed to the fact that the "Sponge reef" facies did not develop in that area until the lower Kimmeridgian.

OCCURRENCE. The material collected by the author came from the Chavoley Beds (Ager & Evamy, 1963) near Virieu-le-Grand (Ain). These beds, consisting of calcareous marls and shales, represent the only argillaceous interruption in the succession of carbonate sediments which constitute the Upper Jurassic of the southern French Jura. The associated fauna included hexactinellid sponges and rare specimens of *Monticarella striocincta*. *L. arolica* was the commonest element in the fauna and is also abundant in the "Birmensdorfer Schichten" of the type area in Switzerland.

Lacunosella vaga sp. n.

(Pl. 2, figs. 1-3, text-fig. 14)

1932 ?*Septaliphoria pinguis* (Roemer); Wiśniewska: pl. 1, figs. 13, 14, NON figs. 1-11, 15-20.

NAME. Latin *vagus-a-um*: wandering, the species has a wide geographical distribution.

DIAGNOSIS. Medium-sized, symmetrical, sub-pentagonal *Lacunosella*; beak small; 16-20 subangular ribs; no posterior smooth area; crura falcifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—only accurately recorded from the upper *mutabilis* and lower *pseudomutabilis* zones.

TYPE SPECIMEN. Holotype, no. BB. 44135, obtained from *mutabilis* zone at Sermérieu (Isère), France.

DIMENSIONS OF HOLOTYPE. Length 2·69 cm, thickness 2·00 cm, width 3·02 cm.

MATERIAL. 43 specimens from type locality; 22 specimens Col du Chat (Savoie); 28 specimens from Franconia. All except the figured specimens are in the author's collection, British Museum (Nat. Hist.) nos. BB. 45668-73, BB. 45756-61.

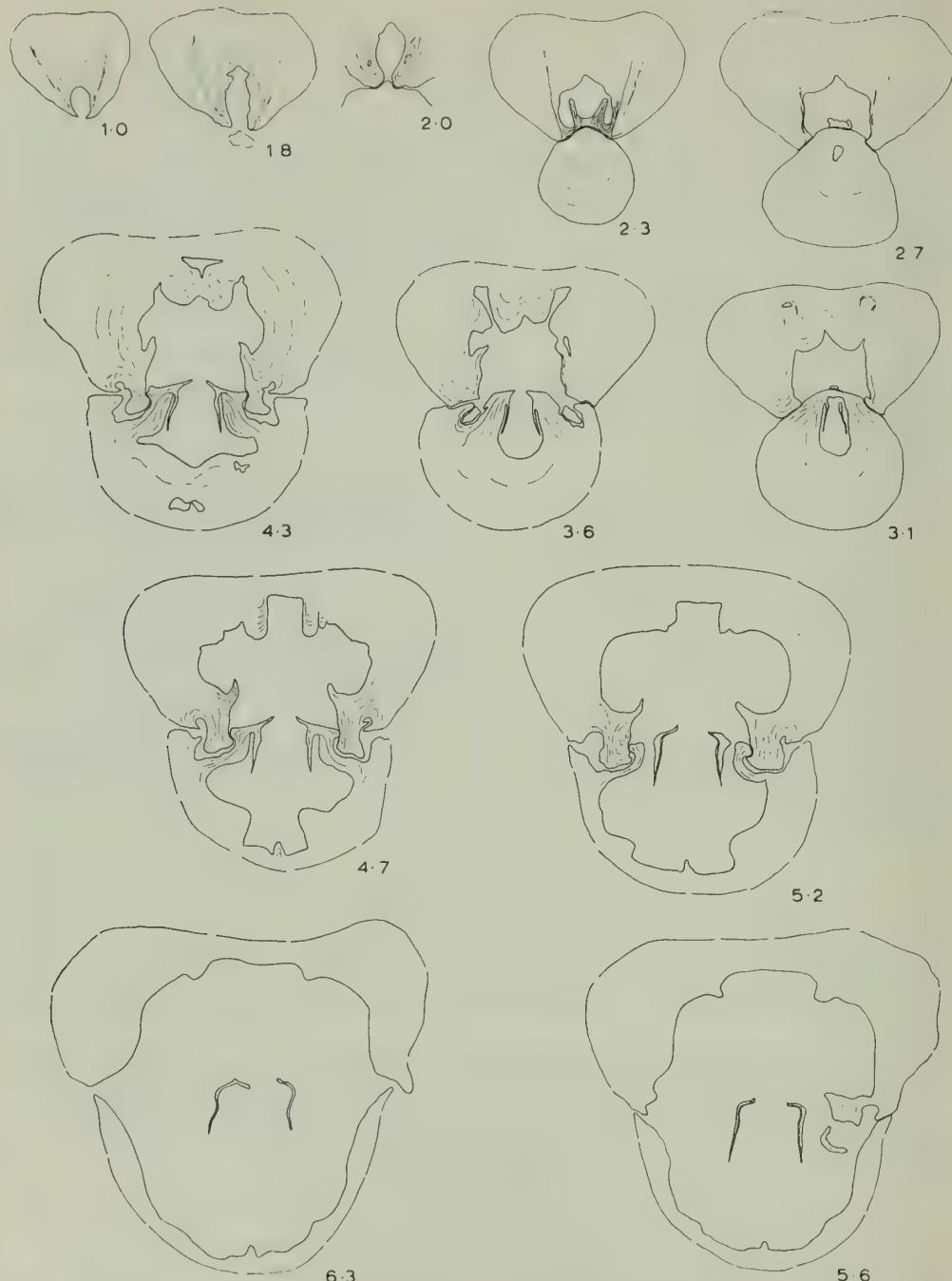


FIG. 12. Transverse serial sections of *Lacunosella arolica* (Oppel). Oxfordian. Chavoley Beds. Virieu-le-Grand (Ain), France. ($\times 3$).

DESCRIPTION. *External characters.* *L. vaga* is weakly trilobate with a low, symmetrical uniplication in the anterior commissure. The brachial is the more inflated valve and the species is generally characterised by a rather globose appearance. Concentric ornament is only rarely present and consists of weak growth lamellae and numerous fine growth lines. The beak is typically small and suberect; conjunct deltidial plates delimit the small submesothyridid pedicle opening. Beak ridges and an interarea are present but only poorly developed.

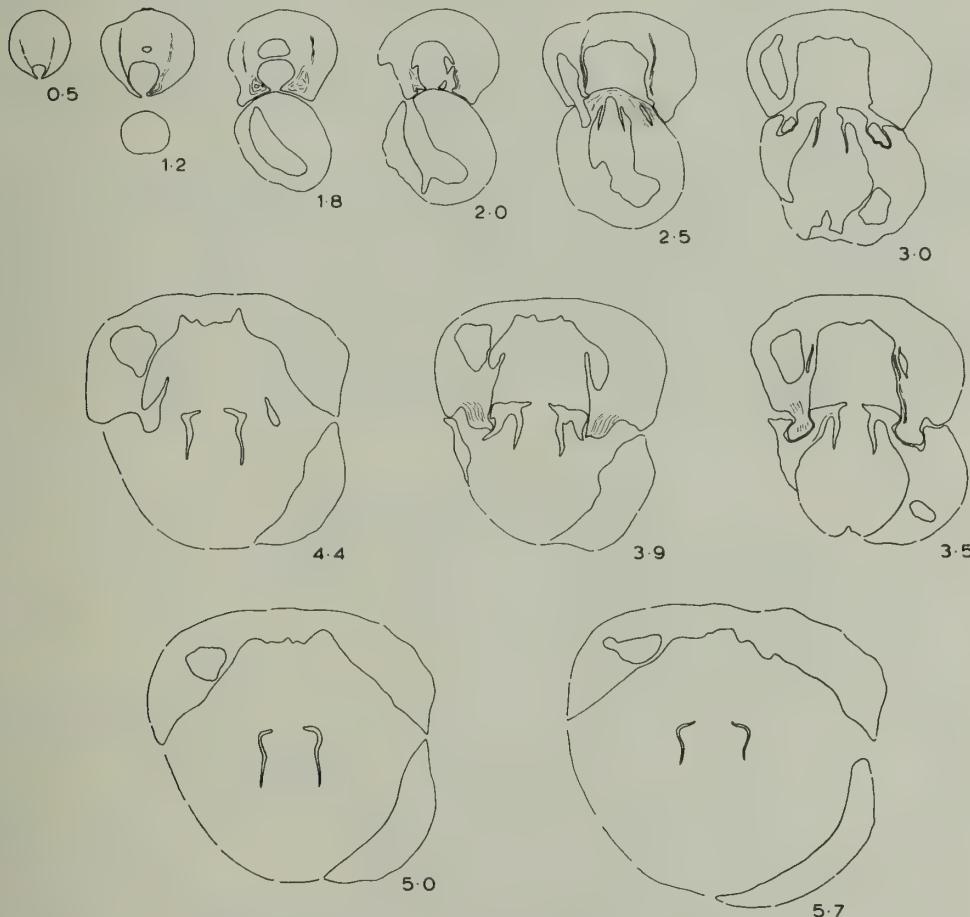


FIG. 13. Transverse serial sections of *Lacunosella arolica* (Oppel). Oxfordian. Chavoley Beds. Virieu-le-Grand (Ain), France. ($\times 3$).

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.69 cm	2.00 cm	3.02 cm
2.84 cm	1.84 cm	3.06 cm
2.78 cm	1.90 cm	2.97 cm

Internal characters. *Pedicle valve.* Shell massive and the muscle impressions deeply inserted. The teeth are strongly developed and lateral denticulae are present.

Brachial valve. Typical lacunosellid falcifer crura are developed. Very strong inner and outer socket ridges are present.

DISTRIBUTION. The species has been collected by the author from the southern French Jura in the Départments of Savoie and Isère and from the Franconian Jura. Two of the specimens from Poland figured by Wiśniewska (v. synonymy) as *Septaliphoria pinguis* are externally identical with *L. vaga* and, as they also come from the same horizon, it seems very likely that Wiśniewska misattributed them. This suggestion is borne out by the fact that Róyzicki (1948) recorded *S. pinguis* sensu Wiśniewska from sponge reefs. If this is the case, then the geographical distribution of the species would be considerably extended.

OCCURRENCE. At the type locality, *L. vaga* is associated with *Torquirhynchia* cf. *astieriformis* and details of the locality are given under that species. The specimens collected from the Col du Chat (Savoie) were from fine-grained, bioclastic limestones. This record is interesting in that it is the only occurrence of *Lacunosella* known to the author where the genus is not associated with sponges; many of the specimens were crushed and the only other fossils collected from the locality were terebratulids. The Franconian material was found with the typical association of sponges, ammonites, terebratulids and lamellibranchs at the base of a small reef.

Lacunosella cracoviensis (Quenstedt) (Pl. 2, figs. 5–6, text-fig. 15)

- 1871 *Terebratula trilobata cracoviensis* Quenstedt: 136, pl. 40, fig. 43.
- 1871 *Terebratula lacunosa subsimilis* (Schlotheim); Quenstedt: 129, pl. 39, fig. 78.
- 1917 ?*Rhynchonella cracoviensis* (Uhlig); Rollier: 172.
- 1917 *Rhynchonella prosimilis* Rollier: 174.
- 1932 *Lacunosella cracoviensis* (Quenstedt); Wiśniewska: 41–46, pl. 2, figs. 6–20.

EMENDED DIAGNOSIS. Medium-sized, subpentagonal *Lacunosella*; prominent narrow, suberect beak; 17–25 fine, bifurcating ribs; crura falcifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian—Lower Kimmeridgian; in Swabia and Franconia it has been recorded from the “beta” and “gamma Malm” while Wiśniewska gives its range in Poland as “Sequanien”.

TYPE SPECIMEN. Lectotype, here selected, fig. 43, pl. 60 in Quenstedt (1871), from the “Coralrag” of Przegorzały, Poland.

MATERIAL. 7 specimens, collection of Tübingen University from Swabia; 21 specimens, author’s collection from Franconia and Swabia, in the British Museum (Nat. Hist.) nos. BB. 45650–67, BB. 45674–77.

DESCRIPTION. *External characters.* *L. cracoviensis* is a medium-sized *Lacunosella*; although the outline is subpentagonal, it shows considerable variation and either length or width may be the greater dimension.

The subangular ribs are relatively fine, commence at the umbones and are often bifurcate. The anterior commissure is usually symmetrical with a low uniplication

developed but not uncommonly it shows varying degrees of asymmetry. There are usually 8–9 ribs on the fold.

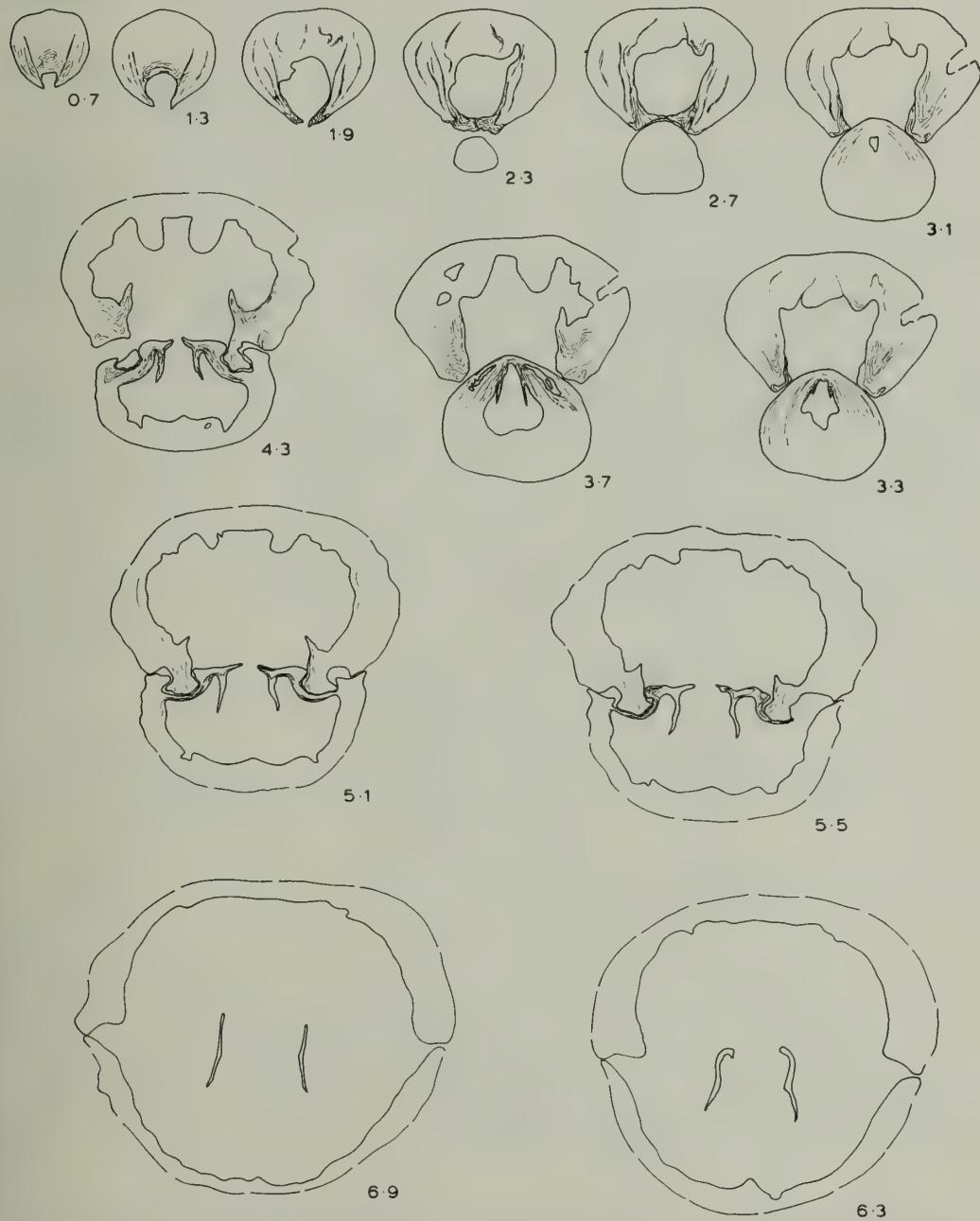


FIG. 14. Transverse serial sections of *Lacunosella vaga* sp. nov. Topotype. Kimmeridgian—*mutabilis* zone. Sermérieu (Isère), France. ($\times 3$).

The suberect beak is narrow and characteristically pronounced. The interarea and beak ridges are scarcely developed. The submesothyridid pedicle opening is small and flanked by conjunct deltoidal plates.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.62 cm	1.40 cm	2.50 cm
2.76 cm	1.97 cm	2.94 cm

Internal characters. Pedicle valve. The shell is massive ; lateral cavities are not developed as the dental lamellae do not appear to touch the ventral shell wall. A pedicle collar is present. The teeth are strongly developed and lateral denticulae are present.

Brachial valve. The falcifer crura are exceptionally wide distally. Inner and outer socket ridges are very strongly developed.

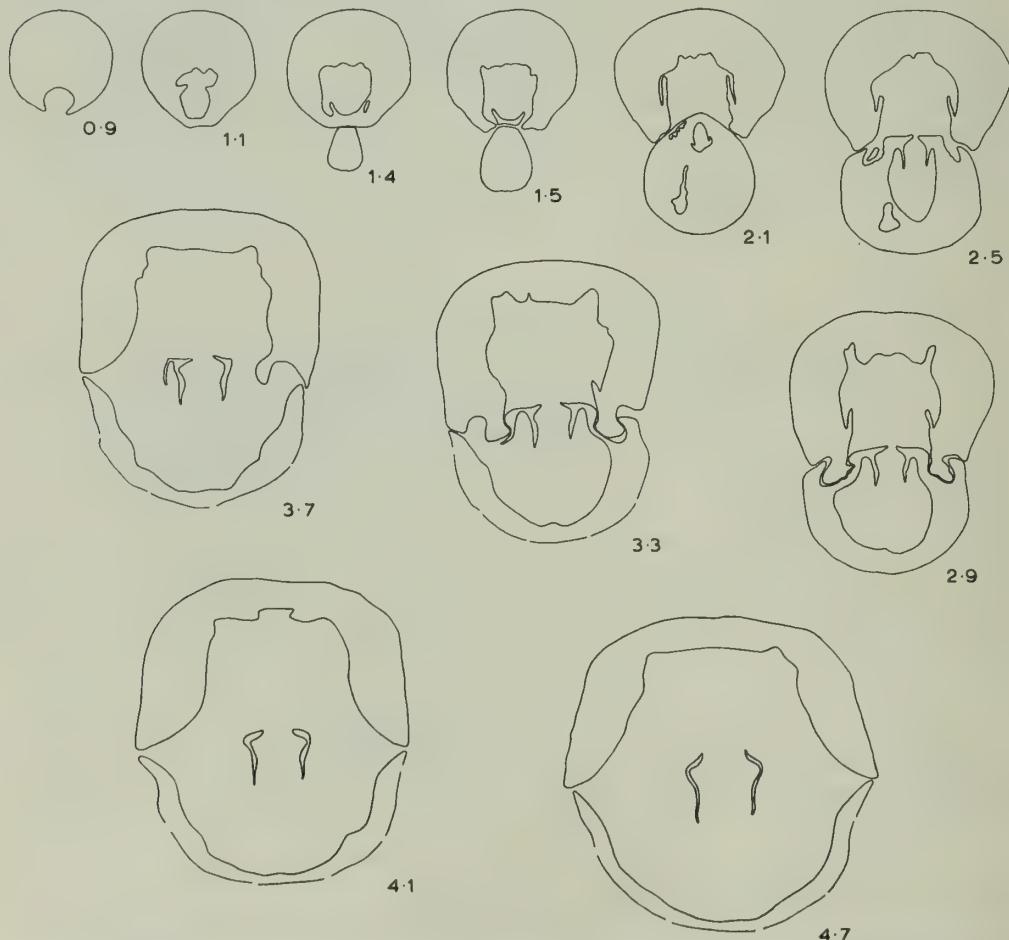


FIG. 15. Transverse serial sections of *Lacunosella cracoviensis* (Quenstedt). "Malm beta/gamma". Würgau, Germany. ($\times 4$).

DISTRIBUTION. The species is recorded from Poland, and the Swabian and Franconian Jura.

OCCURRENCE. Occurs in association with sponge reefs, together with the usual fauna of ammonites and terebratulids.

REMARKS. The name *cracoviensis* was first used by Quenstedt (1871) in describing material from the area of Krakow, Poland ; the specimen he then figured, pl. 60, fig. 43, has been selected as lectotype. The species has been well figured by Wiśniewska (1932) and the author would agree with her in placing in synonymy the specimen figured by Quenstedt (1871), pl. 39, fig. 78, as *Terebratula lacunosa subsimilis* from the "Malm beta". This latter specimen undoubtedly belongs to this rather variable species and other German material from this horizon can be matched exactly with the specimens figured by Wiśniewska from Poland.

The name *subsimilis* was coined by Schlotheim (1820) for material from the "Hornstein", near Amberg, which is generally assumed to be "Malm epsilon" in age. Quenstedt figured a specimen of *subsimilis* of this age (pl. 39, fig. 108). Rollier (1917) proposed the name *prosimilis* for the specimen figured by Quenstedt from the "Malm beta" in order to differentiate it from *subsimilis* of Schlotheim. No specimens from the "Malm epsilon" referable to the Schlotheim species have been examined. It has been decided, in view of the stratigraphic diastem, namely "Malm upper gamma" and "delta" which separates it from *L. cracoviensis*, together with the fact that lack of material makes taxonomic revision impossible, to continue to regard *subsimilis* as a separate species restricted to the "Malm epsilon".

***Lacunosella sparsicosta* (Quenstedt)**
(Pl. 2, figs. 7-8, text-fig. 16)

- 1858 *Terebratula lacunosa sparsicosta* Quenstedt: 633-34, pl. 78, figs. 19-22.
 1871 *Terebratula lacunosa sparsicosta* Quenstedt: 126-28, pl. 39, figs. 92-93, ?94.
 1890 *Rhynchonella lacunosa* var. *sparsicosta* (Quenstedt); Haas: 51-52, pl. 6, figs. 9-12, 15-17.
 1917 *Rhynchonella sparsicosta* (Quenstedt); Rollier: 140.

EMENDED DIAGNOSIS. Small to medium-sized, subpentagonal *Lacunosella*; 6-7 ribs anteriorly of which 2-3 lie on the fold; posterior smooth area present; crura falcifer.

STRATIGRAPHICAL RANGE. It appears to be restricted to the "Malm gamma", which is equivalent to the *cymodoce* zone of the Kimmeridgian.

TYPE SPECIMEN. Lectotype, here selected, fig. 93, pl. 39 in Quenstedt (1871), from the "Malm gamma" of Käsbühl, Germany.

MATERIAL. 10 specimens, author's collection from Franconia in British Museum (Nat. Hist.) nos. BB. 45640-49. 35 specimens, collection of Tübingen University from Swabia; 13 specimens, collection of the Naturhistorisches Museum, Basel, from the Schaffhausen area.

DESCRIPTION. *External characters.* *L. sparsicosta* is one of the smallest species in the genus; it is subpentagonal in outline and has a strong uniplication in the anterior commissure. It is biconvex with the brachial valve considerably more

inflated than the pedicle. The most frequent number of ribs developed is seven, of which three lie in the fold ; these latter ribs are coarse and subangular, contrasting with the lower more rounded ones occurring laterally. There is a posterior smooth area, as the ribs do not originate from the umbones ; the central ribs are, however, developed much further posteriorly than the lateral ones. The ribs are mostly simple. Growth lamellae are usually present but are very variably developed.

The beak is small and suberect. A small, submesothyridid pedicle opening is flanked by small, conjunct deltidial plates. The interarea and beak ridges are only very poorly differentiated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.61 cm	1.03 cm	1.73 cm
1.98 cm	1.93 cm	2.23 cm

Internal characters. *Pedicle valve.* There is a well-developed pedicle collar. The shell is massive and the dental lamellae are only poorly developed so that lateral cavities are hardly present. The delthyrial cavity is subquadrate and ventrally the depressions of the muscle attachment areas can be clearly seen. The teeth are strong and lateral denticulae are present.

Brachial valve. Inner and outer socket ridges are both well-developed. Other features are as described for the genus.

DISTRIBUTION. The species ranges from the northern Franconian Jura through the Swabian Jura to the Schaffhausen area of Switzerland.

OCCURRENCE. The author has only collected the species from one locality, namely Barrenberg in Franconia. The exposure there was not very good but appeared to represent perireefal limestones which had been broken up and the resulting angular blocks recemented. *L. sparsicosta* was the commonest element in a rich fauna which also included sponges, ammonites, *L. cracoviensis*, *Monticarella strioplicata* 'normal' terebratulids and the sulcate terebratulid *Nucleolata*.

Lacunosella trilobata (Zieten)

(Pl. 3, figs. 3-6)

- 1832 *Terebratula trilobata* Münster; Zieten: 56, pl. 42, fig. 3.
- 1832 *Terebratula inaequilatera* Goldfuss; Zieten: 56, pl. 42, fig. 4.
- 1845 *Terebratula trilobata* Zyszner: pl. 5, figs. 1-5.
- 1870 *Rhynchonella trilobata* Moesch: 145, pl. 14, fig. 33.
- 1871 *Terebratula trilobata* Quenstedt: 134-36, pl. 40, figs. 35-39, ?figs. 40-44.
- 1890 *Rhynchonella trilobata* (Zieten); Haas: 55-58, pl. 7, figs. 3-6.
- 1917 *Rhynchonella trilobata* (Zieten); Rollier: 175.
- 1917 *Rhynchonella inaequilatera* (Zieten); Rollier: 176.
- 1918 *Stolmorhynchia trilobata* (Zieten); Buckman: 46.
- 1932 *Lacunosella trilobata* (Zieten); Wiśniewska: 32.

EMENDED DIAGNOSIS. Medium-sized, elongated *Lacunosella* ; very strongly trilobate or asymmetrical ; 17-24 rather shallow, subangular ribs of which 6-9 lie on the fold.

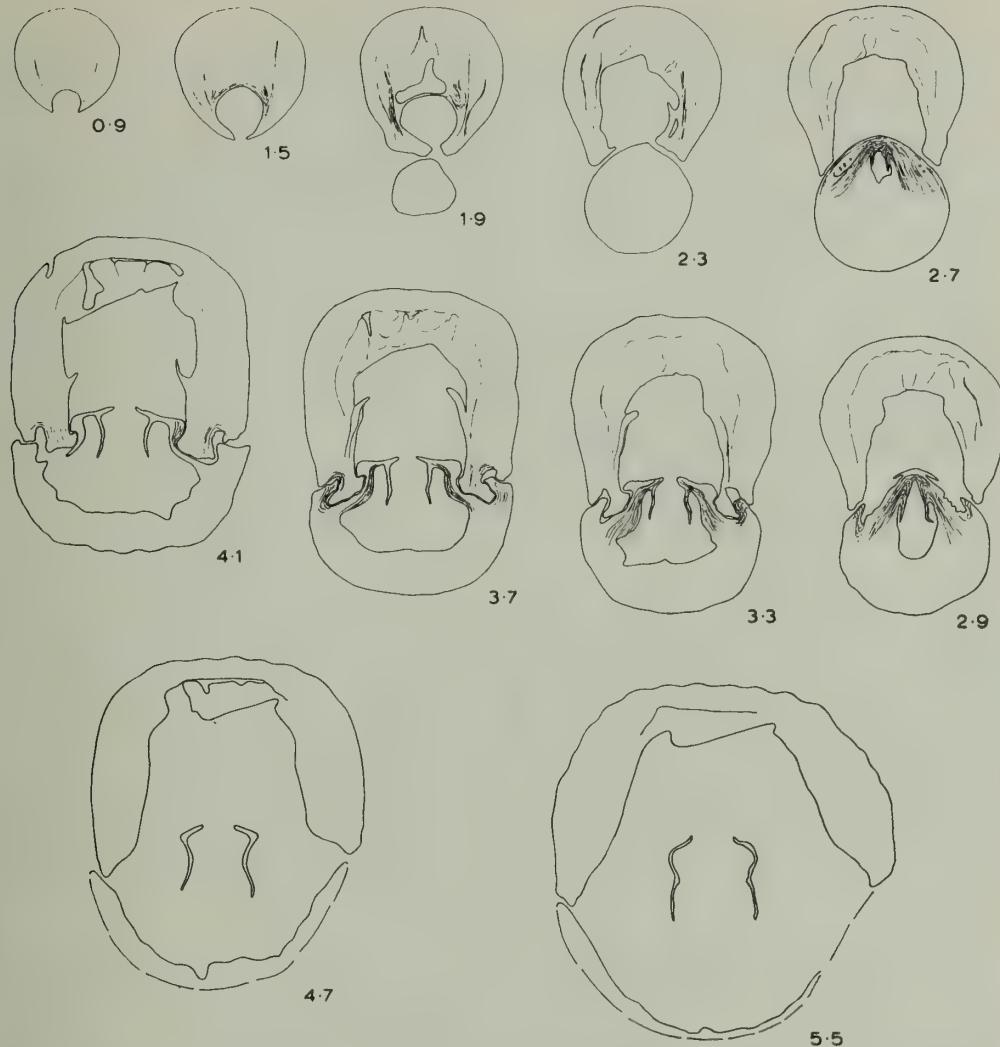


FIG. 16. Transverse serial sections of *Lacunosella sparsicosta* (Quenstedt). "Malm gamma". Barrenberg, Germany. ($\times 4$).

STRATIGRAPHICAL RANGE. The species has only been recorded from the "Malm epsilon" i.e. Lower Volgian.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Zieten, pl. 42, fig. 3. Although Zieten attributes the species to Münster, the reason for this is not known as there does not appear to be any publication of Münster's prior to Zieten in which the species is mentioned. Sherborn (1930) throws no light on the matter, attributing *speciosa* to "von Münster in Zieten". Similarly, there seems no reason for his attribution of *Terebratula inaequilatera* to Goldfuss.

MATERIAL. 2 specimens from the collection of the University of Tübingen; 1 specimen from the collection of the Naturhistorisches Museum, Basel, coming from

the "Kimmeridgian of Württemberg"; 5 specimens in author's collection from the "Malm epsilon" of Franconia, in the British Museum (Nat. Hist.) nos. BB. 45750-54.

DESCRIPTION. *External characters.* The most striking feature of the species is the very marked trilobation shown by most specimens. The species appears to be unique, at least in the upper Jurassic, in that it shows a complete gradation of forms between trilobate symmetrical and bilobed strongly asymmetrical forms. Especially in the trilobate specimens, the brachial valve tends to be considerably the more inflated.

The bifurcating ribs vary considerably in number and development; generally their coarseness is inversely proportional to the number present. The concentric ornament, when present, consists of numerous fine growth lines. The beak is small and flanked by weakly developed beak-ridges; the interarea is slightly incurved. The small pedicle opening is limited by conjunct deltoidal plates.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3.06 cm	2.25 cm	2.80 cm
2.85 cm	2.05 cm	3.19 cm
2.85 cm	1.63 cm	2.78 cm
3.46 cm	2.55 cm	3.21 cm

Internal characters. These were not investigated as the author's collection contains only a very limited number of sufficiently well preserved specimens.

DISTRIBUTION. The species appears to be restricted to the Swabian and Franconian Jura and the Schaffhausen area of Switzerland.

OCCURRENCE. The specimens collected by the author were obtained from well-bedded, fine-grained limestones; they were the most abundant element in a fauna which also included ammonites and sponges. The fact that so few complete specimens were obtained is a result of the extremely hard, brittle nature of the host rock.

Lacunosella sp.

Specimens have been selected from material in the collection of the University of Tübingen in order to conform as nearly as possible to the specimens figured by Quenstedt (1858, 1871) as *Terebratula lacunosa multiplicata* (pl. 3, fig. 1) and *T. lacunosa decorata* (= *Rhynchonella pseudodecorata* of Rollier) (pl. 1, fig. 13). The author has not personally collected material referable to this species and as there is only a very limited amount available at Tübingen, it has not been possible to give full descriptions. "*Rhynchonella*" *pseudodecorata* is of particular interest as it has been selected by Makridin (1955) as the type of his genus *Isjuminella* (= *Isjuminella*). As this species seems to be externally a typical member of *Lacunosella*, it is considered that Makridin probably misidentified his material as his description of its internal structures excludes it from that genus.

Also figured is a specimen of *L. selliformis* (Lewiński) (pl. 2, fig. 4) from the Oxfordian of Poland and a specimen of *L. trilobataeformis* Wiśniewska (pl. 3, fig. 2). The latter is strongly homoeomorphic with *Somalirhynchia moeschi* and these two species appear to have been frequently confused in the past.

Family **RHYNCHONELLIDAE** Gray, 1848
 Subfamily **RHYNCHONELLINAE** Gray, 1848
 Genus **RHYNCHONELLA** Fischer, 1809

- 1809 *Rhynchonella* Fischer: 35.
 1918 *Rhynchonella* Fischer: Buckman, 57.
 1920 *Eurhynchonella* Leidhold: 352.
 1932 *Rhynchonella* Fischer; Wiśniewska: 13.
 1957 *Rhynchonella* Fischer; Ager: 1-15.
 1960 *Rhynchonella* Fischer, Makridin: 252.
 1964 *Rhynchonella* Fischer; Makridin: 111-13.
 1965b *Rhynchonella* Fischer; Ager: H610.

REMARKS. It is not proposed to revise the generic description as the type species, *R. loxiae*, does not occur in western Europe and within this area the genus is only represented by rare and very variable "species". *R. loxiae* has recently been described and figured by Ager (1957) and Makridin (1964).

In Britain, there are only two described Jurassic "species" and very little material which can be referred to *Rhynchonella* s.s. The two species are *R. portlandica* Blake and *R. subvariabilis* Davidson; the type of the former was collected from the Lower Portland Sand of "Black Ven" Portland, and of the latter from the Kimmeridge Clay of Potterne, Wilts. Most of the material referable to *Rhynchonella* has been obtained from the "Rhynchonella Marls" and various horizons in the Portland Sand exposed on the Dorset coast. Apart from this, there are two specimens from the Lydite Bed of Long Crendon, Buckinghamshire, and six specimens from the Kimmeridgian Boulder Beds of Sutherland. Material from these horizons is very scarce and the author is indebted to the curators of the Geological Museum, Oxford, the Sedgewick Museum, Cambridge, and the B.M.(N.H.), for allowing him to use the specimens in their collections.

An interesting series of specimens collected by Prof. M. R. House from the Upper Blackmore Beds, Portland, is figured on plate 4. As these were collected from the same horizon and locality, it can be reasonably assumed that they represent a single variable species. The variation ranges, however, between end-members, which, if they occurred separately and without intermediate forms, would undoubtedly be referred to *R. portlandica* and *R. subvariabilis*. This suggests that perhaps all the British material from this area should be referred to a single species. However, it is considered that further stratigraphically accurately located material is needed before the full range and variation can be determined; until then it seems pointless to try and define taxonomic groups within this plexus of forms which is at present represented by less than thirty specimens, of which few are complete. It is interesting to note that Blake (1880) in proposing his species *R. portlandica*, commented, "One can scarcely feel quite certain whether this is a distinct species from *R. subvariabilis*".

Specimens were collected by the author from the Boulder Beds of Sutherland, and appear to be the first record of the genus from that area. Again, as with the material from the Dorset coast, it does not seem helpful to propose further taxa until more specimens are available.

Makridin (1964) figured several species and subspecies of *Rhynchonella* and a table giving the stratigraphical ranges of these is given below (text-fig. 17); the strati-

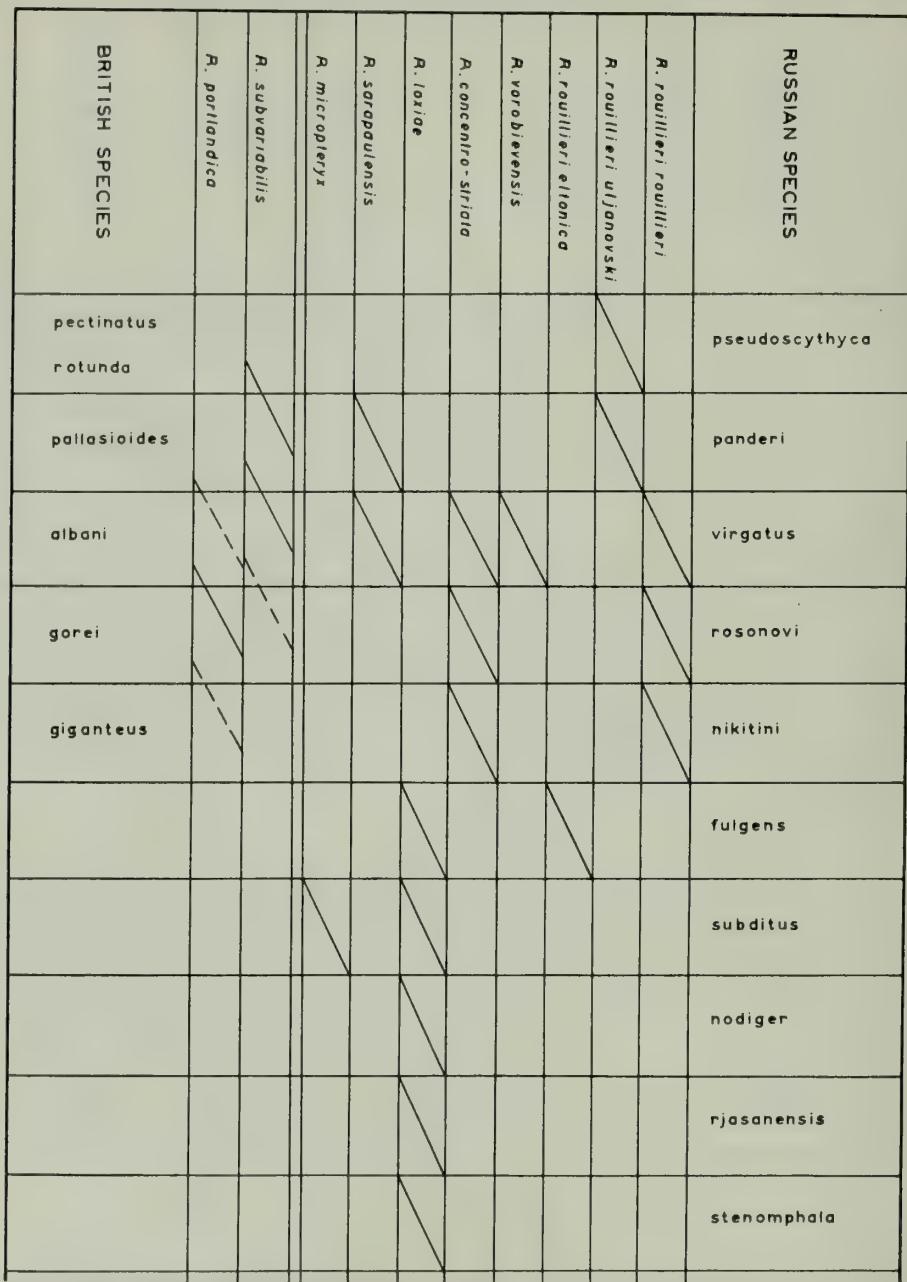


FIG. 17. The stratigraphical ranges of the Russian and British species of *Rhynchonella* s.s.
Details of the Russian species are taken from Makridin (1964).

graphical range of the British *Rhynchonellas* s.s. is also indicated. Some of the forms figured by Makridin from the Russian Platform seem to be quite close to British specimens although the variation of the genus was such that none of the forms from these two areas is considered to be conspecific.

The most distinctive British element seems to be the form with a long, posterior smooth stage and strong, short ribs anteriorly. This form is represented in the specimens collected by Prof. M. R. House, mentioned above, and is the basis on which such species as *R. rivelensis* and *R. triplicosa* are included in the genus. These species are all characterized by the above features and seem to comprise a persistent stock which is first seen in the basal Callovian and continues to the Volgian. It appears that the form represented by *loxiae* and *portlandica* is restricted to the Volgian.

***Rhynchonella rivelensis* Loriol**
(Pl. 5, figs. 3–6, text-fig. 18)

1904 *Rhynchonella rivelensis* Loriol: 282–83, pl. 26, fig. 43.

EMENDED DIAGNOSIS. Small to medium sized *Rhynchonella*; subpentagonal in outline; slightly incurved interarea; large smooth area posteriorly about 10 strong, subrounded ribs anteriorly; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—upper *transversarium* and lower *pseudocardata* zones.

TYPE SPECIMEN. Lectotype, here selected, fig. 43, pl. 27 of Loriol (1904), the specimen came from the “Argovien II” of Mont Rivel, France.

MATERIAL. 60 specimens from Alex near Oyonnax (Ain); 2 specimens from Choux du Dombief (Jura). All the material was collected by Dr. Enay and subsequently donated to the author.

DESCRIPTION. *External characters.* *R. rivelensis* is subpentagonal in outline and is either equally biconvex or with the brachial valve the more inflated. There is a low uniplication in the anterior commissure and a low fold on the brachial valve. A linguiform extension is only poorly developed. The coarse, simple ribs are only developed on the anterior half to one third of the shell; concentric ornament consists of growth lamellae, most clearly seen on the posterior smooth area, and very fine growth lines.

The beak is small, suberect and sharply pointed. Beak ridges are present and limit the incurved interarea. The deltidial plates project slightly around the hypothyridid pedicle opening.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·16 cm	0·66 cm	1·22 cm
1·17 cm	0·77 cm	1·25 cm

Internal characters. Pedicle valve. The quadrate delthyrial cavity is bounded by long subparallel dental lamellae; the lateral cavities are well developed. The teeth are strong but lateral denticulae are scarcely differentiated.

Brachial valve. There is a long, low median septum; septalial plates are not developed. Inner and outer socket ridges are both present. The clearly marked crural bases are sharply pointed; the radulifer crura become expanded distally.

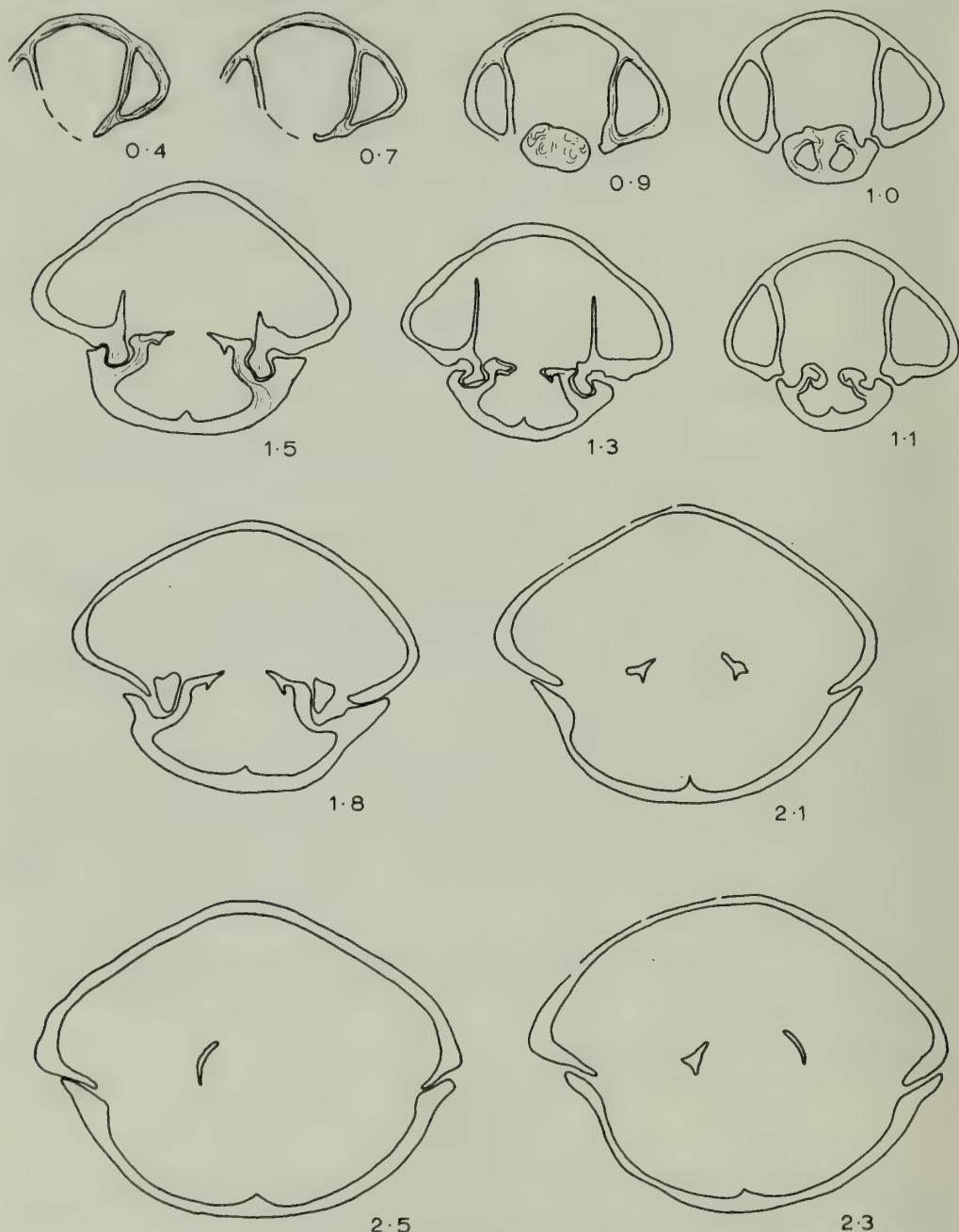


FIG. 18. Transverse serial sections of *Rhynchonella rivelensis* Loriol. Oxfordian—*transversarium* zone. Alex près Oyannax (Ain), France. ($\times 8$).

DISTRIBUTION. The only records of the species are from the central French Jura (Jura lédonien).

OCCURRENCE. Nothing is known except that the material supplied by Dr. Enay came from a pale coloured marl, as evidenced by the adhering matrix.

Rhynchonella sp.

(Pl. 5, figs. 1-2)

REMARKS. The species has not been named or described as only four specimens are known ; these were donated to the author by Dr. D. A. B. Pearson from the Callovian of Kozlowagora in Poland.

Subfamily **IVANOVIELLINEAE** Makridin, 1964

EMENDED DIAGNOSIS. Small to medium sized rhynchonellids ; strong, subangular to rounded ribs ; posterior smooth area ; well marked uniplication and linguiform extension often well developed ; septalium present ; crura calcarifer.

STRATIGRAPHICAL RANGE. ?Pliensbachian—middle Oxfordian.

Genus **THURMANNELLA** Leidhold

- 1920 *Septaliphoria* (*Thurmannella*) Leidhold, pp. 357-62.
- 1964 *Thurmannella* Leidhold; Makridin, pp. 143-44.
- 1965b *Thurmannella* Leidhold; Ager, pp. 609-10.

TYPE SPECIES. The nominal type species is *Terebratula Thurmanni* Voltz which was designated by Makridin. However, this is regarded by the author as a synonym of *Terebratula obtrita* Defrance and is discussed under the latter species.

EMENDED DIAGNOSIS. Small to medium sized, subpentagonal, rhynchonellids ; ventral valve flattened while the brachial is strongly inflated ; 15-22 simple, subrounded to subangular ribs which do not arise at the umbones so that there is a characteristic but variably developed smooth area posteriorly ; well developed uniplication ; linguiform extension usually present but variably developed ; beak small, suberect and sharp ; pedicle opening present ; crura calcarifer.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* to lower *transversarium* zones.

SPECIES. *T. acuticosta* sp. nov.

T. obtrita (Defrance) (1828, pp. 161-62).

DISTRIBUTION. *Thurmannella* has been recorded from northern France, the northern French Jura, the area around Basel and from Yorkshire and Kent. It is not recorded from Germany.

REMARKS. A diagnosis only has been given as a full description is given of the type species, *T. obtrita* ; and a generic description would only differ in being broadened to include *T. acuticosta*, which differs from *T. obtrita* in having a very limited posterior smooth area, more angular ribs and a more strongly developed uniplication in the anterior commissure.

Thurmannella was first established by Leidhold (1920) as a new subgenus within his new genus *Septaliphoria*. The close relationship thus suggested for *Septaliphoria* and *Thurmannella* is based on their both possessing a septalium. It would appear

that *Thurmannella* was not officially elevated to generic rank until Makridin did so in 1964 ; it is also described as a genus in the Anglo-American " Treatise " and the author would certainly agree with its separation from *Septaliphoria*.

***Thurmannella obtrita* (Defrance)**

(Pl. 5, figs. 7-9, text-fig. 19)

- 1828 *Terebratula obtrita* Defrance: 161-62.
 1833 *Terebratula Thurmanni* Voltz; Thirria: 172, 179.
 1842 *Terebratula Thurmanni* Voltz; Boyé: 17, pl. 2, fig. 17.
 1859 *Terebratula Thurmanni* Voltz; Oppel: 608.
 1861 *Terebratula Thurmanni* Etallon: 291, pl. 13, fig. 6.
 1865 *Terebratula Thurmanni* Ogérien: 656, 661, text-figs. 294-296.
 1871 *Terebratula Thurmanni* Voltz; Quenstedt: 90-91, pl. 38, figs. 83-87.
 1882 *Rhynchonella Thurmanni* (Voltz); Haas and Petri: 238-240, pl. 7, figs. 14-17.
 1884 *Rhynchonella obtrita* (Defrance); Deslongchamps: 337, pl. 38, figs. 1-3.
 1889 *Rhynchonella obtrita* (Defrance); Haas: 12-13.
 1897 *Rhynchonella Thurmanni* (Voltz); Loriol: 143-46.
 1900 *Rhynchonella Thurmanni* (Voltz); Loriol: 135, pl. 6, fig. 53.
 1901 *Rhynchonella Thurmanni* (Voltz); Loriol: 112, pl. 6, figs. 17-19.
 1904 *Rhynchonella Thurmanni* (Voltz); Loriol: 283.
 1917 *Rhynchonella Thurmanni* (Voltz); Rollier: 154-56.
 1917 *Rhynchonella silicola* Rollier: 155-56.
 1918 *Rhynchonelloidea thurmanni* (Voltz); Buckman: 38.
 1920 *Septaliphoria (Thurmannella) Thurmanni* (Voltz); Leidhold: 363-65, pl. 5, fig. 6, pl. 6, figs. 10-18.
 1920 *Septaliphoria (Thurmannella) obtrita* (Defrance); Leidhold: 362-65, pl. 5, fig. 5, pl. 6, figs. 1-9.
 1964 ?*Thurmannella thurmanni* (Voltz); Makridin: 135, pl. 6, fig. 53.

EMENDED DIAGNOSIS. As for genus, except that *T. obtrita* always has a well developed smooth area posteriorly.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*mariae* to lower *transversarium* zones.

TYPE SPECIMEN. In view of the great confusion in the literature, it has been decided that it is necessary to erect a neotype in order to fix the species. The specimen proposed was obtained from the " Terrain à Chailles " of Pagny-sur-Meuse (Meurthe et Moselle). This is the horizon and area of Defrance's original specimens. The specimen is in British Museum (Nat. Hist.) no. BB. 44145.

DIMENSIONS OF NEOTYPE. Length 1·40 cm, thickness 1·35 cm, width 1·72 cm.

MATERIAL. 30 specimens from the " Terrain à Chailles ", Pagny-sur-Meuse ; in British Museum (Nat. Hist.) nos. BB. 45720-749. 8 specimens from the " Terrain à Chailles ", Liesdorf, near Basel ; 100 from the *Renggeri* Marl of Arc-sur-Montenot ; 18 specimens from the *Renggeri* Marl of Epeugney ; 30 specimens from the " ferruginous oolite " of the Verdun area.

DESCRIPTION. *External characters.* The smallest specimens are equally bi-convex, have a laterally suboval outline and only a very low uniplication. All these features become considerably modified with growth and in adult specimens the brachial valve is very much the more inflated and generally the uniplication is very

strongly developed ; is it accompanied by the development of a low fold on the brachial valve. However, the development of the uniplication is very variable and it may be low and rounded even in large specimens. The outline of adult specimens is subpentagonal.

The beak is suberect in the young specimens but becomes characteristically erect in the adult ; it is always relatively small and sharply pointed. At all stages the species possesses a well developed, submesothyridid pedicle opening. The beak is flanked by sharp beak ridges which clearly delimit an incurved interarea. The deltoidal plates may be either conjunct or disjunct.

The 15–20 ribs, which are only present on the anterior half to a third of the shell, are low and sub-rounded to sub-angular. The ribs appear to be consistently more rounded on the material from the "Terrain à Chailles" ; however, this may, at least in part, be a result of the different preservation. At the extreme anterior of the largest specimens, the ribs sometimes develop a weak trough along their crests.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·42 cm	1·17 cm	1·53 cm
1·73 cm	1·70 cm	1·93 cm
1·40 cm	1·35 cm	1·72 cm

Internal characters. The specimen sectioned was largely silicified with a consequent loss of much fine detail internally.

Pedicle valve. The subquadrate delthyrial cavity is flanked by strong subparallel dental lamellae, which persist, as seen in transverse section, until the teeth have been completely inserted in their sockets. The teeth do not appear to be crenulated ; lateral denticulae are not developed.

Brachial valve. A septalium is present, although, judging from the sectioned specimen and from the silicified material treated with acid, both the median septum and the septalial plates vary considerably in their development. However, some of this apparent variation is almost certainly a result of the incomplete silicification.

Crural bases are well developed ; inner and outer socket ridges are both present. The crura appear to conform in general appearance with the "calcarifer" type described by Muir-Wood (1936). Distally the cura are blade-like and falciform, as can be seen in text-figure 19, however, at their posterior ends they are bent inwards, at almost right angles to their distal ends, to form a "flange". These "flanges" are undoubtedly the structures Leidhold (1920) figured and described as "Crural-spitze". This feature differentiates the crura from the true falcifer type as developed in *Lacunosella*, and it seems that it is the diagnostic feature of calcarifer crura as defined by Muir-Wood (1936). In her original description Muir-Wood described calcarifer crura as consisting "of two flattened, curved, posteriorly concave laminae which project from the hinge plate into the cavity of the dorsal valve. These laminae each unite with a second curved lamina which appears to be suspended from it and projects dorsally like a spur. A ventral extension of this second lamina terminates in a hook-shaped process, the apex of which is directed medianly".

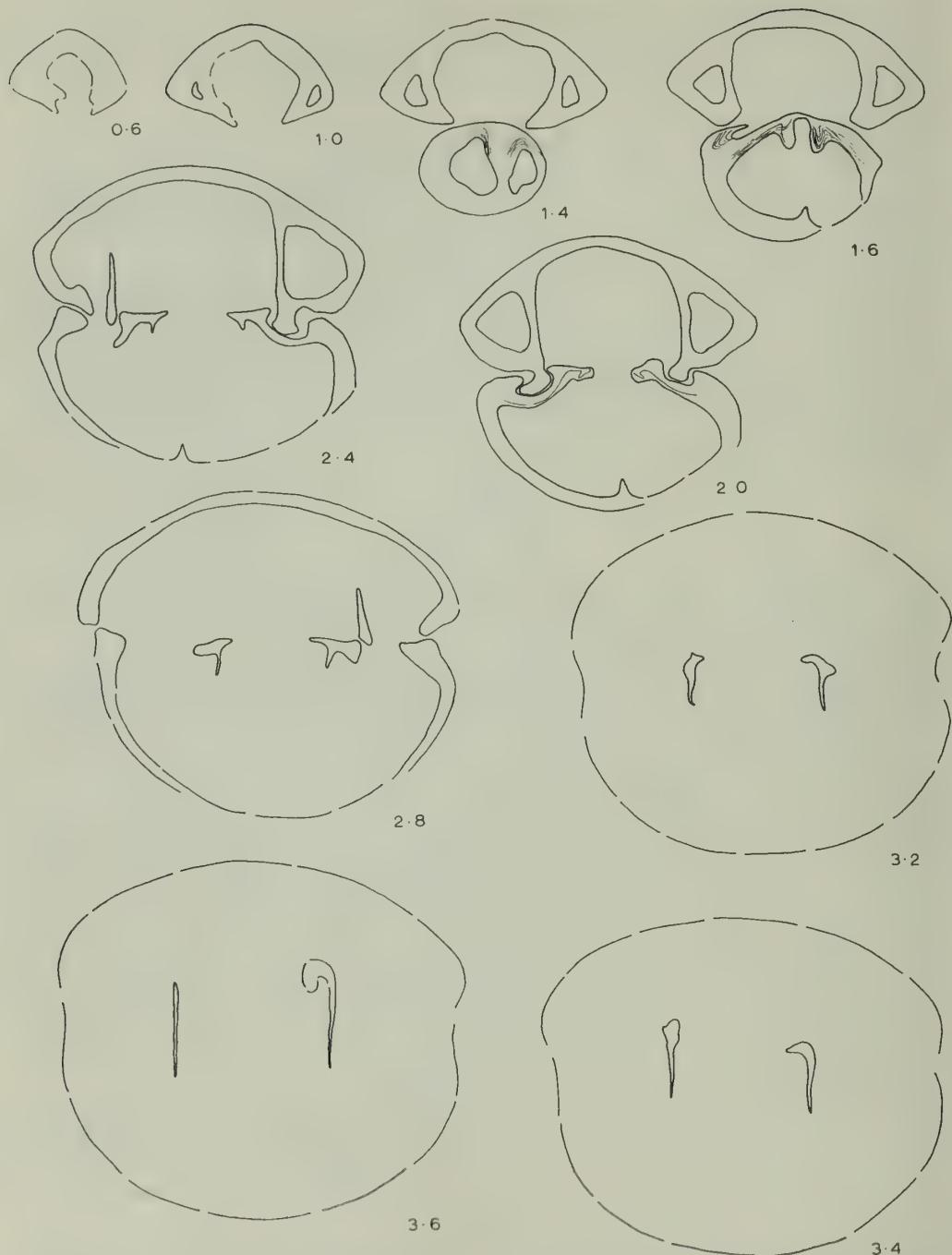


FIG. 19. Transverse serial sections of *Thurmannella obtrita* (Defrance). Oxfordian. "Terrain à Chailles". Pagny-sur-Meuse (Meurthe et Moselle), France. ($\times 5$).

DISTRIBUTION. The species occurs quite widely in the lower Oxfordian of the northern rim of the Paris Basin, in the northern part of the French Jura and in the Swiss Jura around Basel. *T. obtrita* seems to be co-extensive with the "Terrain à Chailles"; whether it is equally widespread within the *Renggeri* Marls is not known, although the remarks of Loriol (1900) would suggest that it is.

OCCURRENCE. The species has been collected in quantity from two horizons represented by three markedly differing lithologies. The lower horizon is represented by the *Renggeri* Marl, which is a dark coloured calcareous clay. The specimens collected showed a very wide range of size and it is presumed that all except the very youngest stages are present. It seems reasonable to assume that the Marl was deposited in a fairly low energy environment.

The *Renggeri* Marl belongs to the *mariae* zone, while the higher horizons at which *T. obtrita* occurs are in the *cordatum* and *transversarium* (lower part) zones. The two distinctive lithologies occurring in the upper zones are the stratigraphically equivalent "Terrain à Chailles", a sandy limestone with nodular layers of silica, and the self explanatory "oolithe ferrugineuse".

The specimens of *T. obtrita* found in the "Terrain à Chailles" tend to be considerably larger than those from the Marls, both in average size and in the absolute size of the largest specimens; it is also noticeable that there are fewer of the very small individuals. It is suggested that the average size of the specimens within the species probably increased through its stratigraphical range and that the larger size of the specimens from the "Terrain à Chailles" is emphasized by the higher energy environments which is assumed from the lithology; the smaller shells were probably carried away.

The "Terrain à Chailles" is coarsely bedded and the tops of the bedding planes are rather nodular and often show evidence of burrowing activity. *T. obtrita* is found predominantly on these nodular surfaces, where it occurs both singly and in groups. Nearly all the specimens are present with complete, articulated shells, suggesting that they were not transported far before burial; this assumption is supported by the very delicate nature of the test.

From the thin shell and the large, obviously functional pedicle opening, it is suggested that the individuals may possibly have lived attached to weed and that on death they became detached and dropped to the bottom. The groups could be either post-mortem accumulations washed together or possibly small colonies which were deposited together from the same fronds of weed; if they in fact adopted that mode of life. The "Terrain à Chailles" deposits are thought to have accumulated in water no deeper than about 10 fathoms and possibly quite close to the shore line.

The above remarks on the "Terrain à Chailles" are probably also largely applicable to the "oolithe ferrugineuse", which is about 7 m thick in the area of Verdun where the specimens were collected. The bed is only poorly exposed, largely in old shell craters, and collecting from it was relatively difficult. *T. obtrita* does not seem to be so abundant as in the "Terrain à Chailles", but the specimens are about the same size. Associated fauna included terebratulids, irregular echinoids (*?Collyrites*), and lengths of *Millerecrinus*.

REMARKS. The considerable confusion as to the correct nomenclature of the species has largely arisen through the inadequacy of the original descriptions. The name *obtrita* was first used in 1828 by Defrance in the " Dictionnaire des Sciences Naturelles "; the description was very generalized and while no figure was given, he referred to plate 241, fig. 5 in the " Encyclopédie Méthodique ". This latter figure is not sufficiently clear for specific identification, although the specimen represented certainly belongs within the *Thurmannella*, *Rhynchonelloidella*, *Ivanoviella* group. While the specimen figured in the " Encyclopédie " is not named or geographically located, in 1820 Schlotheim remarked that it was similar to his *Terebratulites varians*; this fact is also of interest in that the volume of the " Encyclopédie " in which the figure appeared is generally stated to have been published in 1827.

The name *Thurmanni* first appears in Thirria's (1833) work " Statistique Minéralogique et Géologique du Département de la Haute-Saône ", in which the palaeontological identifications were given by Voltz. There is no description or figure and the name only occurs in the faunal lists for the " argile avec chailles " and " marne moyenne avec minerai de fer oolithique ". The first adequate figure of the species is by Boyé (1842) in his " Importance de l'Etude des Fossiles pour la Reconnaissance géologique des Terrains "; again there is no description and the only information given is that *T. Thurmanni* occurs infrequently in " la marne oxfordienne ". Boyé placed this between the " Chailles " and the " Dalle nacrée ", making it almost certainly the " Renggeri Marls " of present nomenclature.

Between 1828 and 1884 the name *obtrita* does not appear to have occurred in the literature, contrasting with *thurmanni* which was widely used, and the species was well figured by several authors under that name. However, in 1884 Deslongchamps published a paper in which he redefined the species originally described by Defrance (1828), using specimens from the Defrance collection. In this work Deslongchamps admitted that the figure in the " Encyclopédie " cited by Defrance was not clear but went on to say that virtually all the specimens of Defrance labelled as *obtrita* belonged to the form subsequently named *thurmanni*. Deslongchamps considered some of the Defrance specimens to have come from the " Terrain à Chailles " of " Bourgogne or Franche Comté ", and not from near Brussels as stated by Defrance, while others came from Lons-le-Saunier, Besançon and Mézières. He then fully described the species, i.e. *obtrita*, and figured three specimens. However, while it is assumed that the figured specimens were from the Defrance collection, this is not certain as a copy of the original work is not available at the British Museum. It is presumed from contemporary synonymies that Deslongchamps produced this paper, with its two plates and their explanations, as a separate publication in 1884.

When the paper on the Defrance species was published in the " Bulletin de la Société linnéenne de Normandie " in 1885, for some reason the explanations to the plates were omitted. From the remarks of Deslongchamps, there seems little doubt as to what Defrance understood by *obtrita* even though this was not clearly stated in his original description. It is presumed that the Defrance collection, which was at Caen, was destroyed together with the Deslongchamps collection during the invasion of Normandy in 1944.

Since the Deslongchamps paper, most authors, with the notable exception of Haas (1889), have continued to use the name *thurmanni*. Rollier (1917) suggested that the name *obrita* should be abandoned and at the same time proposed the restriction of the name *thurmanni* to the smaller forms as typified by the material from the *renggeri* Marl. He placed the larger specimens coming from the "Terrain à Chailles" in a new species *silicola*. To the present author, this arbitrary division seems to have little justification, apart from being inadmissible on the grounds of priority.

In setting up his new subgenus *Thurmannella*, Leidhold (1920) included only two species, namely *T. obrita* and *T. thurmanni*, nominating neither as type of the genus. These two 'species' were differentiated on the grounds that the valves of *T. obrita* were less inflated and that the uniplication was less developed than in *T. thurmanni*; however, as they occur together at the same horizon and localities and as the features mentioned above show complete gradation between the 'end members', it is here considered that Leidhold was in fact dealing with one species. The synonymy given by Leidhold for his two species is interesting in that he placed *T. thurmanni* of Boyé in synonymy with *T. obrita* of Defrance, so separating it from *T. thurmanni* of Voltz; the grounds on which this decision was made are not made clear.

It is concluded that the name *obrita* of Defrance has priority over *thurmanni* of Voltz and that *T. obrita* should be regarded as the type species of *Thurmannella*.

Thurmannella acuticosta sp. n.

(Pl. 5, figs. 10–11, text-fig. 20)

1878 *Rhynchonella varians* var. *Thurmanni* (Voltz); Davidson: 215–16, pl. 28, figs. 14–16.
1933 *Rhynchonelloidea thurmanni* Arkell: 432.

NAME. Latin, *acutus-a-um*—sharp, pointed ; *costa-ae*—a rib ; the species has very sharp ribs.

DIAGNOSIS. Medium sized *Thurmannella* ; about 17–18 relatively coarse, steep, subangular ribs ; possesses only very limited posterior smooth area ; crura calcarifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian—*mariae* zone and lower *cordatum* zones.

TYPE SPECIMEN. Holotype selected is the specimen figured Davidson (1878) pl. 28, fig. 16.

DIMENSIONS OF HOLOTYPE. Length 1·61 cm, thickness 1·46 cm, width 1·74 cm.

DESCRIPTION. *External characters.* The shell outline is subpentagonal to weakly trilobate, the latter condition resulting from the very strongly developed uniplication shown by some specimens. The uniplication in the anterior commissure is emphasized by the strong, steep nature of the subangular ribs. No concentric ornament has been observed.

The beak is sharp and suberect to erect ; the erect condition is much less common than in *T. obrita* and, in comparison with that species, the interarea is smaller and less incurved. An oval, submesothyridid pedicle opening is present ; the details of

the deltidial plates have not been satisfactorily observed. The smooth area on the brachial valve is restricted to not more than the posterior quarter of the valve.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·43 cm	1·10 cm	1·60 cm
1·44 cm	1·12 cm	1·67 cm

Internal characters. The preservation of the available specimens is very poor and it was found that the internal features of the first specimen were completely obliterated by partial silicification. A second specimen was sectioned and the structures,

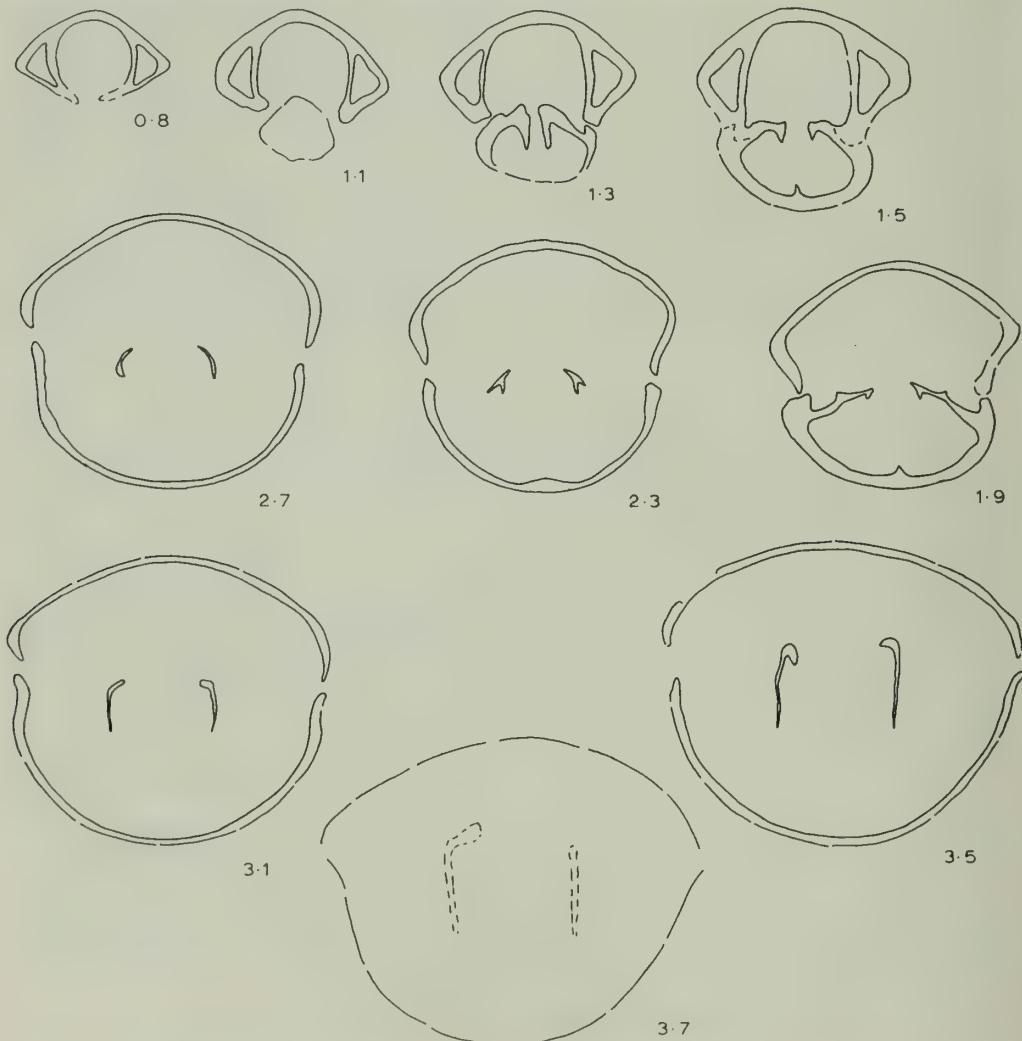


FIG. 20. Transverse serial sections of *Thurmannella acuticosta* sp. nov. Oxfordian. Lower Calcareous Grit. Filey Brigg, Yorks. ($\times 5$).

although still only poorly preserved, appeared to show no notable differences from those described above for *T. obtrita*.

DISTRIBUTION. *T. acuticosta* is one of the most common species in the Lower Calcareous Grit of Yorkshire but, according to Arkell (1933), it has only been recorded from two localities in the south of England, namely, at Catcombe, near Lyneham, and in one of the Kent borings.

OCCURRENCE. The Lower Calcareous Grit appears to be very similar to the "Terrain à Chailles", as developed in the *cordatum* and lower *transversarium* zones of northern France, with the exception of the abundance of "*Spongia paradoxica*" (=the trace fossil *Thalassinoides teste* Ager), as seen at Filey Brigg. It would appear that the environment represented is again of the nearshore, high energy type.

Subfamily ACANTHOTHYRIDINAE Schuchert, 1913
Genus **ACANTHOTHIRIS** Orbigny

- 1850 *Acanthothiris* Orbigny, 323.
- 1875 *Acanthothyris* Orbigny: Paetel, 1.
- 1877 *Acanthothiris* Dall, 11.
- 1886 Gruppe der Spinosen Rothpletz, 93.
- 1889 *Acanthothyris* Orbigny: Buckman and Walker, 41.
- 1894 *Acanthothyris* Orbigny: Hall and Clarke, 836.
- 1914 *Acanthothiris* Orbigny: Buckman, 2.
- 1917 *Acanthothyris* Orbigny: Rollier, 74.
- 1918 *Acanthothiris* Orbigny: Buckman, 70.
- 1929 *Acanthothiris* Orbigny: Schuchert and Le Vene, 26.
- 1936 *Acanthothyris* Orbigny: Muir-Wood, 27.
- 1960 *Acanthothiris* Orbigny: Ager, 157.
- 1960 *Acanthothiris* Orbigny: Makridin, 256.
- 1963 *Acanthothiris* Orbigny: Seifert, 168.
- 1965b *Acanthothiris* Orbigny: Ager, H611.

TYPE SPECIES. *Terebratulites spinosus* Schlotheim, designated by Rollier (1917). This is regarded by the author as a synonym of *Anomia spinosa* Linnaeus (1767) and is discussed below.

EMENDED DIAGNOSIS. Small to medium sized sub-pentagonal or laterally oval rhynchonellids; biconvex; uniplicate with low dorsal fold; many well developed ribs, several of which bifurcate; test covered by hollow spines which arise from the crests of the ribs; beak small and erect or slightly incurved; well developed groove ("pedicle trough") running from posterior of pedicle opening to tip of beak; fairly strong median septum present; crura radulifer.

STRATIGRAPHICAL RANGE. ?Aalenian, Bajocian—Bathonian/basal Callovian.

DESCRIPTION. *External characters.* The larger acanthothirids tend to be more globose than the smaller; the brachial valve is more inflated than the pedicle. The many well marked, rather shallow, sub-rounded ribs tend to bifurcate laterally and from their crests arise the long, slender, hollow spines which cover the test. There is a slight fold on the dorsal valve and a rounded uniplication in the anterior commissure. The beak is relatively small and sufficiently incurved to obscure the

details of the pedicle opening and deltoidal plates. Beak ridges and interarea are present but rather variable in development. The young forms tend to be subtrigonal to subcircular.

Internal characters. *Pedicle valve.* The delthyrial cavity is quadrate in transverse section, but in the initial posterior sections there is a low dorsally directed ridge. This results from the presence of a groove which is situated on the antero-dorsal side of the beak and runs from the pedicle opening to the tip of the beak. This structure appears to be a pedicle collar as originally defined by Thomson (1927); it is not, however, the structure defined as a pedicle collar in the "Treatise" (1965), and is here referred to as the "pedicle trough".

The lateral cavities are relatively narrow and the slender dental lamellae bounding them are either subparallel or slightly divergent ventrally. Teeth and sockets are both crenulated.

Brachial valve. A median septum is quite well developed. A septalium is not present but the median structure, dorsal of the ventrally arched hinge plates, seen in *A. spinosa* and *A. cf. A. costata* could possibly have resulted from the fusion of septalial plates. Crural bases are hardly differentiated. The crura are of the radulifer type and tend to be oval or flattened in the plane of articulation, as seen in transverse section. Muscle scars have not been observed and even Buckman (1918) commented that they were obscure in both valves.

SPECIES. As well as *A. spinosa* and *A. cf. A. costata*, here described, the literature abounds with descriptions and names of spinose rhynchonellids of this age. The following nominal species are provisionally attributed to this genus :

- A. balinensis* Rollier (1917, p. 77)
- A. broughensis* Muir-Wood (1952, pl. 123, p. v, figs. 11, 13-15)
- A. crossi* (Walker) (1869, p. 215)
- A. costata* Orbigny (1850, p. 286)
- A. doultningensis* (Richardson and Walker) (1907, p. 426, pl. xxvii, fig. 2)
- A. elargata* Seifert (1963, p. 170, pl. x, fig. 8)
- A. globosa* Buckman (1918, p. 918, pl. xix, fig. 25)
- A. inflata* (Quenstedt) (1868, p. 112, pl. xxxix, figs. 46-47)
- A. midfordensis* (Richardson & Walker) (1907, p. 427, pl. xxvii, fig. 1)
- A. multispinosa* Seifert (1963, p. 172, pl. x, fig. 12)
- A. oligacantha* (Branco) (1879, p. 127, pl. vi, figs. 6-7)
- A. paucispina* Buckman and Walker (1889, pp. 52-53)
- A. powerstockensis* Buckman and Walker (1889, p. 52)
- A. radwanowicensis* Rollier (1917, p. 77)
- A. sentosa* (Quenstedt) (1868, p. 113, pl. xxxix, figs. 55-56)
- A. sinuata* (Quenstedt) (1868, p. 114, pl. xxxix, fig. 59)
- A. subglobosa* Seifert (1963, p. 171, pl. x, fig. 11)
- A. tenuispina* (Waagen) 1867, p. 640, pl. xxxii, fig. 6).

DISTRIBUTION. *Acanthothiris* is a common genus occurring widely throughout the Middle Jurassic rocks of Europe, including those of England, Normandy, the French, Swiss and German Jura and Poland.

OCCURRENCE. The genus has been collected by the author only from coarse, bioclastic limestone.

REMARKS. On account of their distinctive appearance members of *Acanthothiris* have been described and figured on numerous occasions, usually under the name of *Rhynchonella*, *Terebratula* or *Acanthothiris spinosa*. The author has not attempted to disentangle the nomenclature and synonymy of these numerous descriptions and figures, but has here only attempted to define and clarify the type species together with *A. cf. costata*, which happened to be a very common fossil in the part of the southern French Jura mapped by members of Imperial College. The latter species was investigated in order to obtain a wider knowledge of the variation of internal structures of the genus as these are not adequately described in the literature.

***Acanthothiris spinosa* (Linnaeus)**
(Pl. 5, figs. 12–17, text-figs. 21–22)

- 1767 *Anomia spinosa* Linnaeus: 1154.
- 1768 (concha) *anomia ventricosa, striata echinata*, d'Annone in Knorr and Walch: 90, pl. B₄, fig. 4.
- 1779 *Anomia* Walcott: 21, fig. 31.
- 1813 *Terebratulites spinosus* Schlotheim: 73.
- 1813 *Anomia spinosa* Linnaeus; Townshend: 372.
- 1817 *Terebratula spinosa* Smith: 108.
- 1820 *Terebratulites spinosus* Schlotheim: 269.
- 1825 ?*Terebratula aspera* Koenig: fig. 219.
- 1829 *Terebratula spinosa* Townshend and Smith; Phillips: 123, pl. 9, fig. 18.
- 1833 *Terebratula spinosa* Buch: 58–59.
- 1838 *Terebratula spinosa* Buch: 161–62, pl. 6, fig. 4.
- 1850 *Hemithiris spinosa* Orbigny: 268.
- 1850 *Acanthothiris spinosa* Orbigny: 323.
- 1851 *Rhynchonella spinosa* (Schlotheim); Davidson: 71–73, pl. 15, figs. 15–20.
- 1857 *Rhynchonella spinosa* (Schlotheim); Deslongchamps: 355–56, pl. 5, fig. 1.
- 1858 *Rhynchonella spinosa* (Schlotheim); Davidson: 222.
- 1882 *Rhynchonella spinosa* (Schlotheim); Buckman: 40–41.
- 1889 *Acanthothyris spinosa* (Linnaeus); Buckman and Walker: 12–14.
- 1900 *Acanthothyris spinosa* (Schlotheim); Greppin: 178–80, pl. 19, fig. 3.
- 1917 *Acanthothyris spinosa* (Schlotheim); Rollier: 76–77.
- 1918 *Acanthothiris spinosa* (Linnaeus); Buckman: 70–72, pl. 19, fig. 26.
- 1936 *Acanthothiris spinosa* (Linnaeus); Muir-Wood: 28.
- 1936 *Acanthothyris spinosa* (Schlotheim); Arcelin and Roché: 54–58, pl. 1, figs. 1–18, pl. 12, fig. 2.
- 1959 *Acanthothyris spinosa* (Schlotheim); Henry: 119–21.
- 1966 *Acanthothiris spinosa* (Schlotheim); Alméras: 277–79, pl. 17, figs. 1–3.

EMENDED DIAGNOSIS. Medium to large sized *Acanthothiris*; relatively globose; outline subpentagonal; brachial valve considerably more inflated than the pedicle; "pedicle trough" present; well marked uniplication; 30–35 ribs on each valve; crura radulifer.

TYPE SPECIMEN. Neotype, here proposed, is the specimen in the collection of the B.M.(N.H.) from the Inferior Oolite of Rodborough Hill numbered B4030. The

exact horizon is not given but it is probably from the Upper Trigonia Grit, i.e. the *parkinsoni* zone of the Bajocian.

STRATIGRAPHICAL RANGE. Upper Bajocian to Upper Bathonian/Lower Callovian.

DIMENSIONS OF NEOTYPE. Length 2·14 cm, thickness 1·71 cm, width 2·37 cm.

MATERIAL. 30 specimens from the collection of the B.M.(N.H.) ; 23 specimens from Normandy and 9 from Switzerland in the collection of the author in the British Museum (Nat. Hist.) nos. BB. 45682-89.

DESCRIPTION. *External characters.* Medium to large sized *Acanthothiris* which is characteristically fairly globose. In early growth stages the two valves are of almost equal convexity but, in adult forms, the brachial valve is much the more inflated. Young forms have a subcircular to subtrigonal outline, which becomes modified to the subpentagonal shape of the adult. The width is usually, but not invariably, greater than the length. There is a marked, rounded uniplication in the anterior commissure, accompanied by a low fold on the brachial valve.

In early growth stages, the beak tends to be small, acute and erect ; it becomes more incurved in the adult and often obscures the pedicle opening and deltidial plates. The deltidial plates, as seen in the serial sections, are conjunct ; the pedicle opening is submesothyridid. Beak ridges are quite well developed and limit the incurved interarea.

The test ornament consists of about 30 to 35 subangular to subrounded ribs, as counted at the anterior commissure ; these ribs may bifurcate once or twice, rarely more, and occasional ribs are inserted by intercalation. The long, slender spines which form the most distinctive feature of the genus arise from expanded bases situated along the crests of the ribs. Spines of up to 1 cm have been observed still attached to the test ; however, in most specimens they are indicated only by the presence of low spine bases. Although they are hollow, they do not seem to have had any direct connection with the mantle. The other ornament consists of rather weak growth lines, which are usually only seen in the inter-rib troughs of well preserved material, and occasional growth lamellae.

Davidson (1858) suggested that, "when alive, *R. spinosa*, was more or less coloured with red ; at least, we have seen specimens in which the spines had preserved that colour ; this is also the opinion of M. Deslongchamps". This observation was probably founded largely on material from quarries near Caen in Normandy and, while true, omits to point out that large numbers of other organisms are also so coloured and this would appear to be due to some local factor rather than to original colouration. Dr. Rioult, (personal communication, 1964) suggested that this colouration is due to algae.

DIMENSIONS OF FIGURED ADULT SPECIMENS.

length	thickness	width
2·28 cm	1·78 cm	2·37 cm
2·14 cm	1·71 cm	2·37 cm
2·42 cm	2·05 cm	2·88 cm

Internal characters. Pedicle valve. The development of the deltidial plates, showing the crumpling together characteristic of the species, is clearly illustrated in

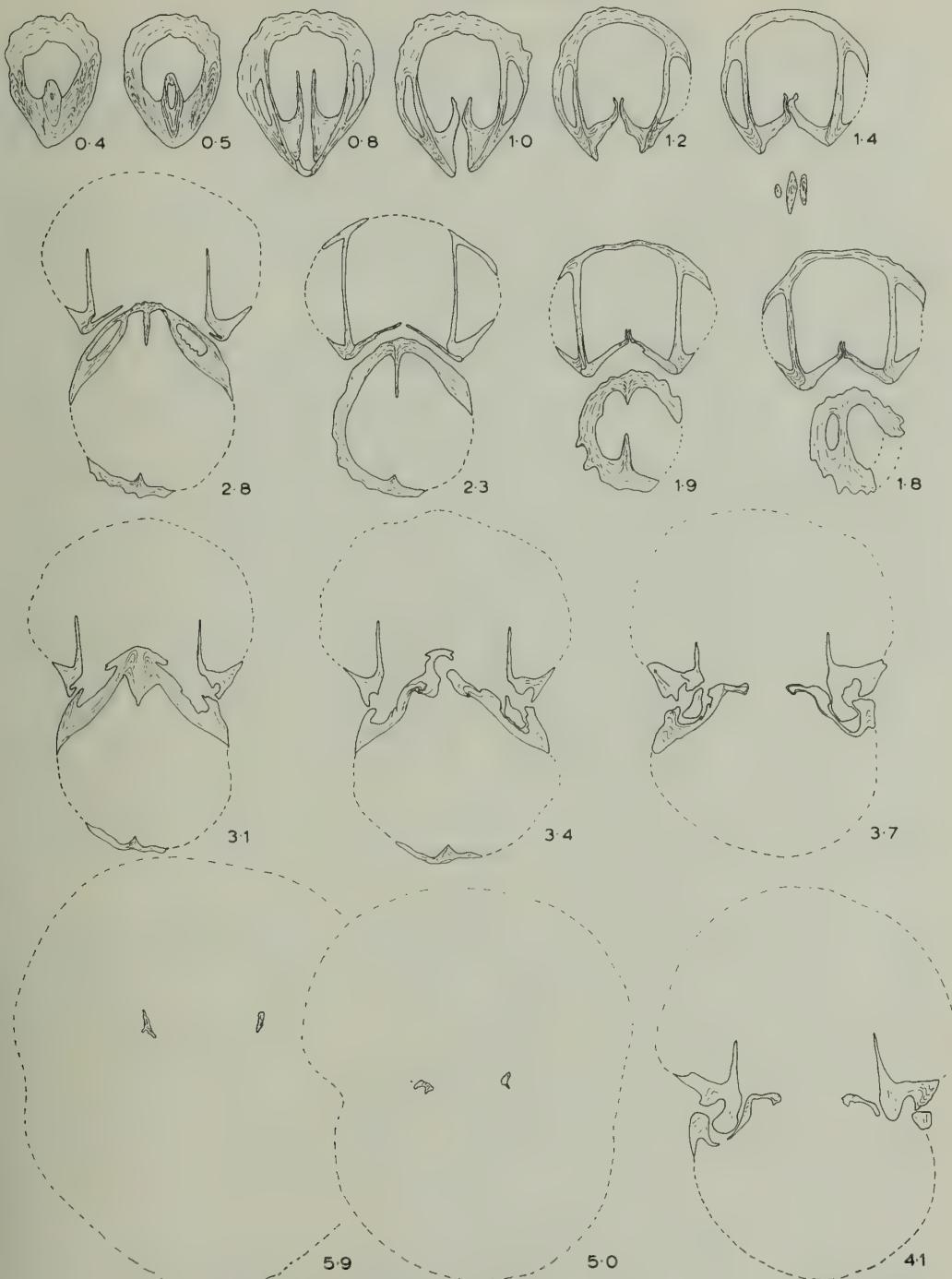


FIG. 21. Transverse serial sections of *Acanthothiris spinosa* (Linnaeus). Bajocian. Upper Trigonia Grit. Wooton-under-Edge, Glos. ($\times 4$).

the serial sections. The pedicle opening can be seen at the base of the pedicle groove ; the difference in appearance of this structure, as compared with *A. cf. costata* results from the greater incurvature of the beak in *A. spinosa*.

Brachial valve. See generic description. The shape of the crura seems to be a useful criterion for differentiating the species from *A. cf. costata*.

DISTRIBUTION. The species has been definitely recorded from the Cotswolds, Normandy, northern France, around Basel in Switzerland and from Monsard (Saône et Loire). The name *spinosa* has been used frequently in the past for any spinose rhynchonellid and consequently from the literature, it is very difficult to ascertain the true distribution of *A. spinosa* s.s.

OCCURRENCE. The species is considered to have lived under conditions similar to those described for *A. cf. costata*.

REMARKS. The rhynchonellid now known as *Acanthothiris spinosa* s.s. was first figured by Knorr and Walch (1768) with the description, "concha anomia, ventricosa, striata echinata", which was given by Professor d'Annene. A specimen regarded by Rollier (1917) as the type of Knorr and Walch is preserved in the Naturhistorisches Museum of Basel ; however, as Rollier pointed out, this specimen differs markedly from the original figure in such features as the number of ribs, of which the specimen has 36-38 on the pedicle valve rather than the 26 figured. This discrepancy is such that Dr. Gasche, of the Museum, is of the opinion (personal communication 1965), that this is not the original of the Knorr and Walch figure and the present author would concur with this observation.

Linnaeus (1767)* described *Anomia spinosa*, stating that it had long spines and that it came from England. Although, unfortunately, the original is not preserved in the Linnaeus Collection, at present in the B.M.(N.H.), it seems reasonable to assume that the *A. spinosa* referred to by Linnaeus is the very common Inferior Oolite species of *Acanthothiris*. This was the view taken by Muir-Wood in her 1936 monograph. Therefore, it has been decided to define the species with a neotype from the Bajocian of the Cotswolds.

The confusion over the authorship of the species has arisen mainly as a result of Schlotheim (1813) mentioning a *Terebratulites spinosus*, which he did not figure or describe, but merely referred to the figure of Knorr and Walch. As this figure was not named in the correct binomial form and as it is regarded by the present author as conspecific with *Anomia spinosa* of Linnaeus, the Schlotheim name must be regarded as a synonym and the species attributed to Linnaeus.

In 1889 Buckman and Walker fully discussed the earlier literature and redescribed all the known British spinose rhynchonellids. Rollier added to the confusion by setting up many new species based purely on published figures, many of which were wholly inadequate in the first place. Buckman (1918) redefined the genus and

* This is the first edition in which *spinosa* is described and at the end of the remarks on habitat, which mention that the species occurs in England, is written "Solander". Daniel Carl Solander was an associate of Linnaeus but it is not clear whether, by placing Solander's name after the remarks Linnaeus was suggesting that he was the author of the species or whether he was merely quoting Solander in stating that the species occurred in England. All subsequent authors who have referred to the "Systema Natura" have attributed the name *spinosa* to Linnaeus.

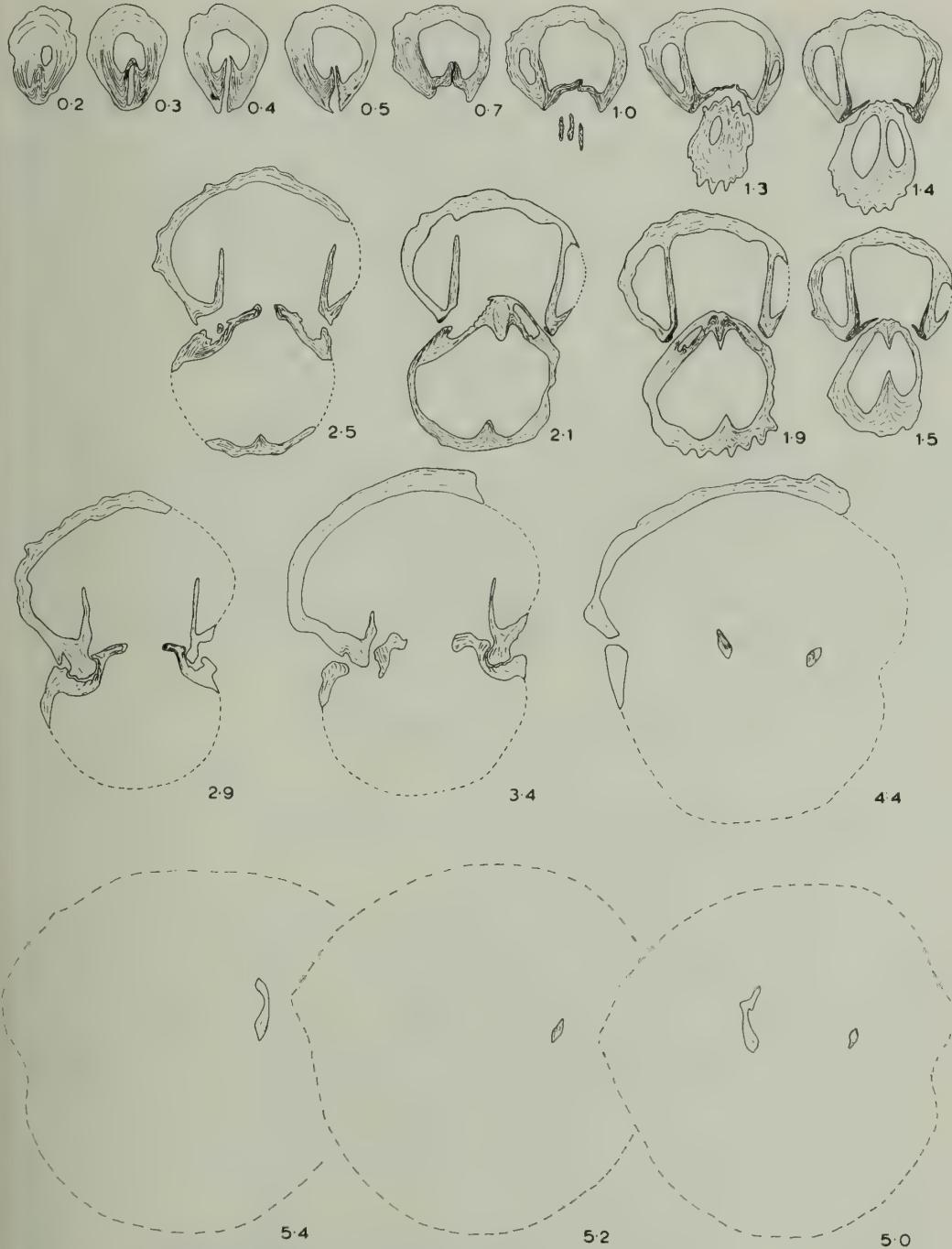


FIG. 22. Transverse serial sections of *Acanthothiris spinosa* (Linnaeus). Bathonian. "Varians Schichten", Liestal, Basel, Switzerland. ($\times 4$).

although no specific description of *A. spinosa* was given, he figured a specimen of *A. spinosa* s.s. from the Inferior Oolite of Midford near Bath.

There was no further discussion of the species until 1936 when Arcelin and Roché attempted to disentangle the synonymy, but failed to take account of the literature prior to Schlotheim. They described and figured a beautiful series of silicified specimens from the Bajocian of Monsard (Saône et Loire) ; these specimens have been examined in the collection of the University of Lyon and appear to belong to *A. spinosa* s.s., although it is difficult to compare the internal structures with those of the sectioned material. Also in 1936 Muir-Wood discussed the type of the genus, concluding it to be the species referred to by Linnaeus and that this was the "common Inferior Oolite species" ; in doing this, however, she appears to have overlooked the earlier designation of Rollier. She also stated that she considered the *spinosa* of Linnaeus to be congeneric but not conspecific with the form described by Knorr and Walch from Muttenz, as specimens from that area were "larger and more globose".

The area of Muttenz now being an industrial suburb of Basel, it is not possible to obtain exactly topotypic material ; however, within a few kilometres there are good exposures of the Upper Bathonian Varians-Schichten from which the original is presumed to have come and the author visited one such exposure at Liestal, collecting a good sample of specimens. From the examination of this material, the author believes that it should be considered as conspecific with the English species from the Inferior Oolite ; specimens from both areas have been sectioned, see text-figs. 21, 22 and are identical internally.

Acanthothiris cf. *costata* Orbigny
(Pl. 6, figs. 2-4, text-fig. 23)

- 1850 *Hemithiris costata* Orbigny: 286-87.
- 1850 *Acanthothiris costata* Orbigny: 323.
- 1910 *Hemithiris costata* Orbigny; Thevenin: 100, pl. 20, figs. 18-20.
- 1917 *Acanthothryris costata* (Orbigny); Rollier: 74.
- 1918 *Acanthothiris costata* Orbigny; Buckman: 71.

EMENDED DIAGNOSIS. Medium sized *Acanthothiris* ; width always greater than length ; outline sub-oval ; 25-30 low, rounded ribs ; beak small and tightly pressed to the brachial valve ; crura radulifer.

STRATIGRAPHICAL RANGE. d'Orbigny's material came from the "Bajocien", while the specimens here described are of Upper Bathonian/Lower Callovian age.

MATERIAL. Numerous specimens collected by the author and various members of Imperial College from the southern French Jura. 20 specimens in the author's collection in British Museum (Nat. Hist.) nos. BB. 45690-45709.

DESCRIPTION. *External characters.* The width is always greater than the length, resulting in a laterally suboval outline. The beak is very small and closely adpressed to the brachial valve ; no pedicle opening or deltoidal plates are visible externally in the adult specimens. Beak ridges and interarea are both poorly developed. Adult specimens have between 25 and 30 ribs, as counted at the anterior

commissure. These ribs are rather rounded in cross section and frequently bifurcate once or twice over their length ; ribs are also occasionally inserted by intercalation. The ornament also includes growth lines, but these are not strongly developed and are only seen on well preserved material. Long, slender spines arise from the crests of the ribs and are fairly evenly distributed over the test ; the hollow nature of these is clearly seen in the serial sections. There is a low rounded uniplication in the anterior commissure ; however, any accompanying fold in the brachial valve is only poorly developed.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.96 cm	1.45 cm	2.57 cm
1.87 cm	1.38 cm	2.50 cm
1.84 cm	1.15 cm	2.30 cm

Internal characters. *Pedicle valve.* The deltidial plates, as seen in serial section, are very weakly developed, as compared with *A. spinosa*, and do not meet and become crumpled together. The nature of the "pedicle trough" is clearly seen but from the incurvature of the valve it could obviously have been functional only during the early stages of ontogeny as proved by the inflation of the brachial valve and the incurvature of the beak which must have lead to atrophy of the pedicle in adults. The dental lamellae diverge slightly ventrally and limit a subquadrate delthyrial cavity. The teeth are strong and crenulated.

Brachial valve. The median septum is quite strongly developed. There is no septalium as the septalial plates, although present, are very weak. Crural bases are not differentiated. The crura are radulifer and curve distally toward the pedicle valve ; at their proximal ends they are rather flattened in cross section and lie in the plane of articulation.

DISTRIBUTION. The material on which Orbigny based his original description came from Gueret (Sarthe) ; all the specimens described by the author came from the southern French Jura (Ain).

OCCURRENCE. Details of the type locality for *A. costata* are not known. The Jura material was collected from the Middle Chanaz Beds (Ager & Evamy, 1963) from the area around Belley (Ain). Dr. Evamy gives the following description of the lithology in his thesis: "irregularly bedded, poorly sorted calc-arenites, characterized . . . by their content of ferruginous ooliths. . . . The lower and principal unit . . . consists of irregularly bedded brown and grey limestones and similarly coloured shales". He also notes, "The member (Middle Chanaz Beds) may also be recognized in the field by the abundance of *Acanthothiris*".

The acanthothirids occurred as clusters or "nests" in the limestones and concentrations of them were also noticed in the shales. In both situations the forms were mainly adult with valves intact and, in the majority of cases, with the beaks pointing downwards. It would seem that most of the specimens were not far removed from their life position ; however, some movement or sorting is indicated by the noticeable lack of juvenile forms and the similar lack of *in situ* spines. It should be noted

that while many of the specimens were in " nests " or associations, either vertical or horizontal, many others occurred singly and scattered through the rock unit. The above mentioned " nests " have been referred to by Ager & Evamy (1963) as seeming, " to be true colonial associations ".

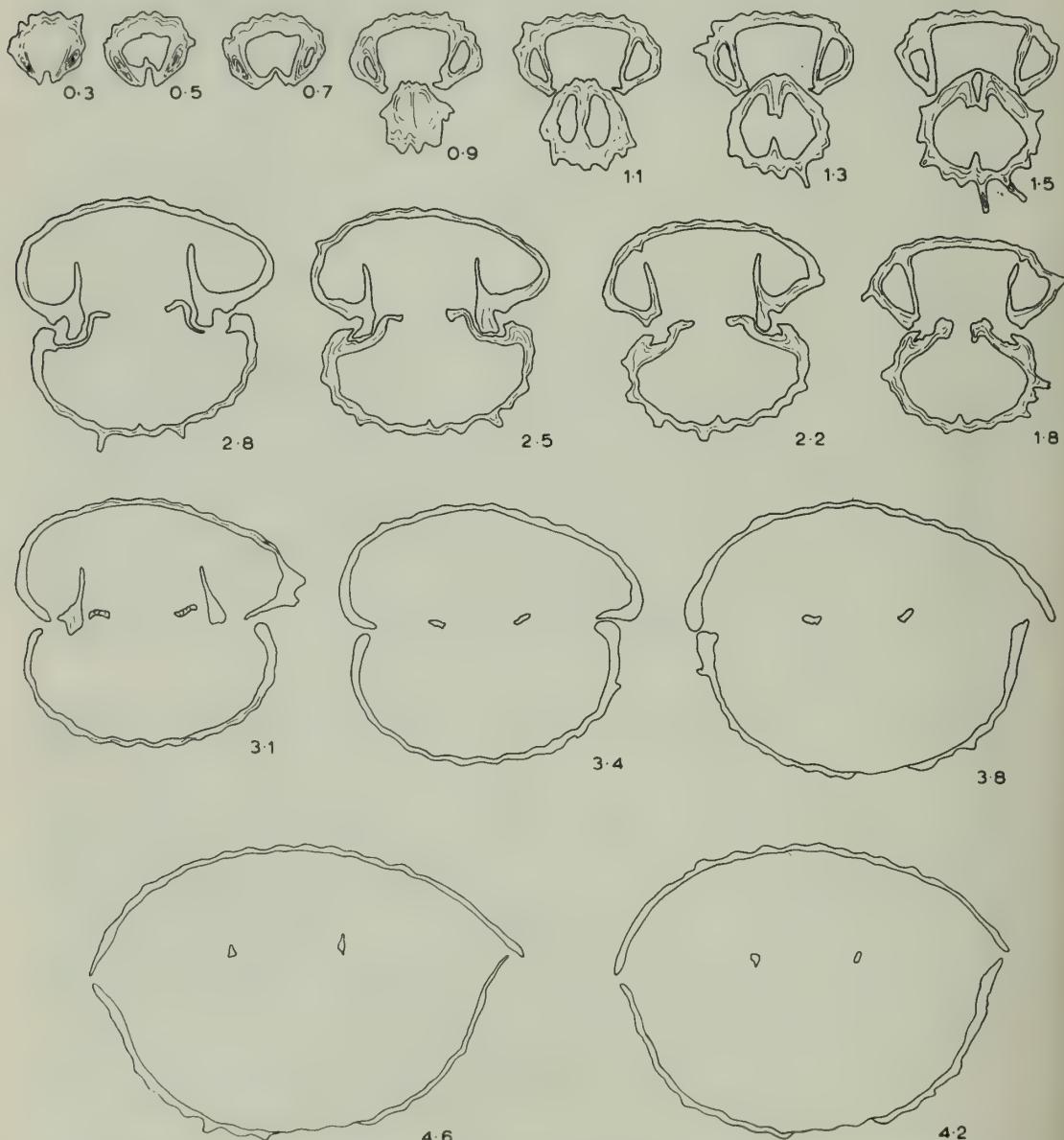


FIG. 23. Transverse serial sections of *Acanthothiris* cf. *costata* Orbigny. Bathonian/Calelovian. Middle Chanaz Beds. Pugieu (Ain), France. ($\times 4$).

The evidence of the lithology is such as to suggest a rather high energy environment. Given that the latter deduction is correct, it seems to the author that the spines would have been a useful anchoring device and it is considered that Rudwick (1964) under-estimated this function in proposing a sensory role for them.

REMARKS. A plaster cast of the specimen from the Orbigny collection figured by Thevenin (1910) has been examined, through the kindness of Dr. Fischer of the Jardin des Plantes (Musée d'histoire Naturelle), and externally this closely resembles the material collected from the southern French Jura. However, a conspecific identification has not been given as no topotype material has been sectioned and hence no comparison of the internal structures has been possible. The main difference between the Orbigny specimen and those described from the Jura lies in the rib count ; that of the former being 20 while that of the latter is between 25 and 30. As the other two specimens of *A. costata* in the Orbigny collection are only poorly preserved (Dr. D. V. Ager, personal communication 1965), it is not considered reasonable to separate the Jura form as a new species merely on the basis of the slight difference in the number of ribs without an investigation of topotype material of the Orbigny species to ascertain its variation and internal structure.

Genus **ACANTHORHYNCHIA** Buckman

- 1914 *Acanthorhynchia* Buckman: 2, (nomen nudem).
 1918 *Acanthorhynchia* Buckman: 69.
 1960 *Acanthorhynchia* Buckman; Makridin: 256.
 1965b *Acanthorhynchia* Buckman: Ager: H611.

TYPE SPECIES. *Acanthothyris panacanthina* Buckman and Walker, by original designation.

EMENDED DIAGNOSIS. Small to medium sized rhynchonellids ; transversely oval or sub-triangular in outline ; thin test covered by numerous fine spine-covered ribs ; anterior commissure rectimarginate or with slight uniplication ; deltidial plates absent, or reduced and disjunct ; crura calcifer or radulifer.

STRATIGRAPHICAL RANGE. Upper Bajocian—Upper Volgian/Neocomian.

DESCRIPTION. *External characters.* The genus contains a series of small to medium sized rhynchonellids. The smaller species tend to be subtriangular in outline, equally biconvex and generally flatter, while the larger species are transversely oval in outline, more globose and with the brachial valve more inflated than the pedicle.

The anterior commissure may have a slight uniplication in the larger forms, but in the smaller it is usually straight. The beak is relatively small and suberect or erect ; deltidial plates are absent in the smaller forms and of a reduced, disjunct variety in the larger. Beak ridges and interarea are never well developed. There are typically one or two well developed growth lamellae, but the finer growth lines have not been observed. The test is covered with many fine, bifurcating ribs, from the crests of which are developed the characteristic, numerous fine spines which project at a low angle.

Internal characters. *Pedicle valve.* The dental lamellae are apparently only developed in the larger species and, when they are not developed, the teeth tend to be inserted at a very shallow angle.

Brachial valve. A low median septum may be present but septalial plates and a septalium are never developed. The ends of the inner hinge plates show a distinctive thickening and in one species, *A. (Acanthorhynchia) spinulosa*, this results in a structure comparable with a cardinal process. The crura, especially in *A. (Acanthorhynchia) panacanthina*, the only really well preserved species examined, appear to closely resemble the form described by Muir-Wood (1935) as calcarifer. However, in other species they seem to more closely resemble the radulifer type.

SPECIES. The following nominal species are provisionally recognized as belonging to the genus ; a sub-generic designation is given where possible :

- A. davidsoni* (Roller) (1917, p. 77)
- A. (Echinirhynchia) dealbata* (Roller) (1917, p. 80)
- A. (Echinirhynchia) fileyensis* (Buckman & Walker) (1889, p. 56)
- A. (Echinirhynchia) impressata* (Roller) (1917, p. 79)
- A. (Echinirhynchia) lorioli* (Roller) (1917, p. 79)
- A. (Acanthorhynchia) multistriata* (Kitchin) (1900, pp. 75-77) pl. xiv, figs. 10, 11
- A. (Acanthorhynchia) myriacantha* (Deslongchamps) (1859, p. 251, pl. iv, fig. 12)
- A. nikitensis* Gerasimov (1955, p. 216, pl. xlivi, fig. 5)
- A. (Acanthorhynchia) panacanthina* (Buckman & Walker) (1889, p. 53)
- A. (Acanthorhynchia) regans* (Szajnocha) (1879, p. 222, pl. vi, figs. 1, 2)
- A. (Echinirhynchia) senticosa* (Schlotheim) (1820, p. 268)
- A. (Echinirhynchia) silicea* (Quenstedt) (1871, p. 115, pl. xxxix, fig. 66)
- A. (Acanthorhynchia) spinulosa* (Oppel) (1858, p. 608)
- A. (Acanthorhynchia) vilsensis* sp. nov.
- A. zieteni* (Roller) (1917, p. 75).

DISTRIBUTION. Although rare, the genus is very widespread and occurs throughout the French and German Jura, and in Normandy, Poland and England. It has also been recorded from the Kutch.

REMARKS AND OCCURRENCE. The genus was founded by Buckman in 1918, after being mentioned by him in 1914. In his original description, Buckman included most of the species here retained in the genus, together with a few now considered as belonging to *Acanthothiris* or to be of uncertain affinity. Although distinctive, all the included species are rather rare and this has necessitated the use of much borrowed material in order to attempt a complete revision of the genus.

The genus *Acanthorhynchia*, as here defined, includes two distinct groups, based on external morphology, which overlap each other in time and, to a lesser extent, geographical area. It is here proposed to designate these groups as sub-genera, namely *Acanthorhynchia* s.s. and *Echinirhynchia* sub-gen. nov.

As stated above, all the species are rare and details of the source rock and supposed environment are only rarely given in the literature. However, the fact that *A. (Acanthorhynchia) panacanthina* comes from the Inferior Oolite and *A. (Acanthorhynchia) regans* comes from the Balin Oolite suggests that the sub-genus *Acanthor-*

hynchia s.s. lived in fairly high energy environments. The specimens of *Echinirhynchia* collected from the French Jura came from very fine-grained sediments, either clays or calclutites, while the material recorded from Germany is also either from clays e.g. *Terebratula senticosa impressae* Quenstedt, or from the sponge reef facies e.g. *A. (Echinirhynchia) senticosa* (Schlotheim). The occurrence of the sub-genus in these two markedly different facies may possibly indicate that its mode of life was planktonic or that it lived attached to floating weed ; this hypothesis was suggested by Ager (1965a).

Sub-genus *ACANTHORHYNCHIA* s.s.

TYPE SPECIES. *Acanthothyris panacanthina* Buckman and Walker.

DIAGNOSIS. Medium to large species of *Acanthorhynchia* with a transversely oval to subrounded outline ; either equally biconvex or with a more inflated brachial valve ; deltidial plates and dental lamellae may be present.

STRATIGRAPHICAL RANGE. Upper Bajocian—Upper Volgian/Neocomian.

DISTRIBUTION. The sub-genus has a wide range both geographically and chronologically ; however, the consistent external and internal features of the included species suggest a continuous evolutionary lineage. The extent of the geographical range is given under the species description. Apart from the species described *A. (Acanthorhynchia) multistriata* (Kitchin) is recorded from the "Oomia Group" of the Kutch and *A. (Acanthorhynchia) rogans* (Szajnocha) occurs in the "Balin Oolite" of Poland.

A. (Acanthorhynchia) panacanathina (Buckman and Walker)

(Pl. 6, figs. 5–7, text-fig. 24)

- 1851 *Rhynchonella senticosa* (Buch); Davidson: 73–74, pl. 15, fig. 21.
- 1878 *Rhynchonella senticosa* (Buch); Davidson: 223.
- 1878 *Rhynchonella senticosa* (Buch); Davidson: 85, pl. 4, fig. 20.
- 1882 *Rhynchonella senticosa* (Buch); Buckman: 41–42.
- 1889 *Acanthothyris panacanathina* Buckman and Walker: 53–54. [= *A. Davidoni* Rollier 1917].
- 1918 *Acanthorhynchia panacanathina* Buckman and Walker; Buckman: 69–70, pl. 19, fig. 23. [= *A. Davidoni* Rollier 1917].

EMENDED DIAGNOSIS. Large *Acanthorhynchia* which ranges in size up to 3·05 cm long, 2·20 cm thick and 3·53 cm wide. Biconvex and transversely suboval in outline ; beak suberect ; deltidial plates narrow, trigonal and disjunct ; anterior commissure sinuate ; crura calcifer.

STRATIGRAPHICAL RANGE. Bajocian—probably restricted to the *parkinsoni* zone.

TYPE SPECIMEN. In their synonymy Buckman and Walker (1889) mention the specimen figured by Davidson (1851) on pl. 15, fig. 21 and it seems reasonable to take this as the type of the species. B 12082 (B.M. (N.H.))

DESCRIPTION. *External characters.* This is the largest known species of *Acanthorhynchia*. The test is covered with fine ribs ; Buckman and Walker cite a specimen as having about a hundred ribs on each valve, with forty spines on each rib. This statement seems to be essentially correct, although the fineness of the features concerned is such as to preclude accurate counting except on well preserved and

JURASSIC RHYNCHONELLIDS

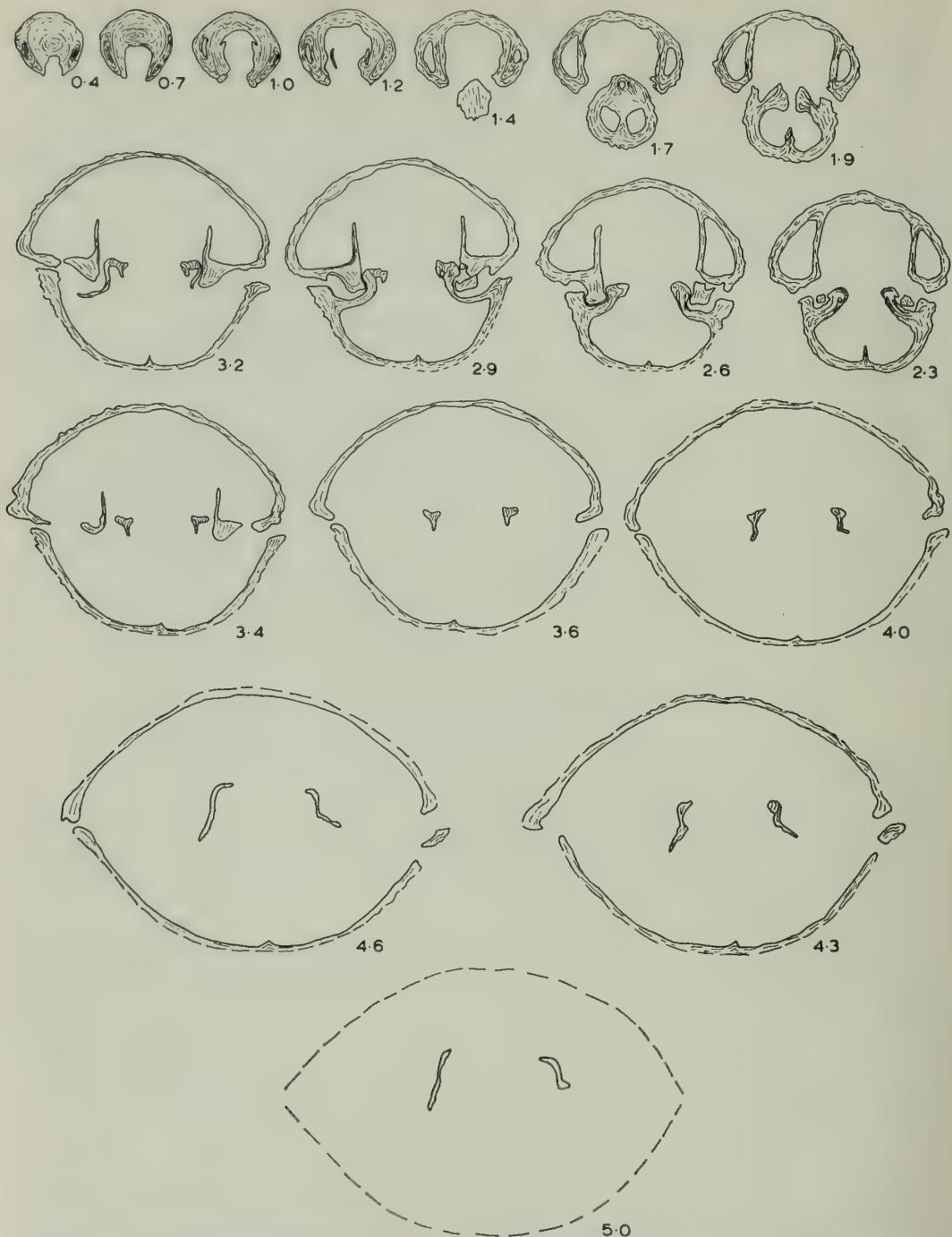


FIG. 24. Transverse serial sections of *A. (Acanthorhynchia) panacanthina* (Buckman & Walker). Topotype. Bajocian. Burton Bradstock, Dorset. Specimen donated by the B.M.(N.H.). ($\times 4$).

carefully prepared material. The ribs maintain a consistent spacing over the surface by constant dichotomy.

The shell is biconvex with the brachial valve the more inflated of the two. The beak is small and suberect. Disjunct trigonal deltidial plates flank the elliptical submesothyridid pedicle opening. Typically there are one or two well developed growth lamellae, although the "very numerous fine growth lines", noted by Buckman (1918) have not been observed on the material studied. The shell being very thin and delicate, short, slightly diverging dental lamellae and a short median septum are frequently seen, in pedicle and brachial valves respectively, of worn specimens.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1.40 cm	0.68 cm	1.55 cm
3.05 cm	2.20 cm	3.53 cm
2.46 cm	1.73 cm	2.66 cm

Internal characters. *Pedicle valve.* The deltidial plates are only poorly developed, as seen externally, but in serial section they are seen to line the subquadrate delthyrial cavity laterally. Near the umbo, sections 1.0 to 1.2 in text-fig. 24 are seen two thin concave lamellae forming a weak pedicle collar. The dental lamellae are quite strong and parallel to one another, not breaking away from the ventral shell wall, as seen in serial section, until the teeth are fully inserted in their sockets; the lateral cavities are always relatively small.

Brachial valve. There is a long, low median septum. Septalial plates are not developed but there is a very distinctive thickening of the inner ends of the hinge plates, as shown in plate 12. This thickening possibly served for anchoring the didductor muscles. Lateral denticulae are present but, in common with the inner and outer socket ridges, are not well differentiated. The crura seem to be quite close to the shape described by Muir-Wood (1934) as calcarifer.

DISTRIBUTION. The author has not collected personally any material of this species and, therefore, it seems reasonable to quote the distribution given by Buckman and Walker (1889, p. 54) in their original description of the species: "This species appears to be confined to the district south of the Mendip Hills. It is a rare fossil, and it occurs only in the *parkinsoni* zone. It is, however, widely distributed, and has been obtained in Dorset, at Burton Bradstock, Broadwindsor, Clifton Maybank, Bradford Abbas, Halfway House and Combe Quarry near Sherborne. In Somerset, at Misterton, Haselbury and at Crewkerne Station". The B.M.(N.H.) material, on which this revision is based, confirms this distribution. The species has not been recorded in the literature outside Britain and the only possible occurrence known to the author is represented by a few poorly preserved specimens collected by him from the *parkinsoni* zone of Normandy.

OCCURRENCE. No details were given by Buckman and Walker, but as the species seems to be restricted to the Inferior Oolite, it presumably lived in a fairly high-energy environment. The material in the collection of the B.M.(N.H.) shows quite

a wide range in the size of the individuals and as they are very well preserved this would indicate that they had not been carried far, if at all, before being buried.

A. (*Acanthorhynchia*) *spinulosa* (Oppel)
(Pl. 6, figs. 8-9, text-fig. 25 (top))

- 1850 *Hemithiris senticosa* (pars) Orbigny: 375.
 1857 *Rhynchonella spinulosa* (pars) Oppel: 608.
 1904 *Acanthothyris spinulosa* (Oppel); Loriol: 284-85, pl. 27, fig. 44.
 1917 *Acanthothyris spinulosa* (Oppel); Rollier: 79.

EMENDED DIAGNOSIS. Medium sized *Acanthorhynchia*; transversely oval in outline; anterior commissure rectimarginate or with very slight uniplication; beak small and incurved; beak ridges and interarea present.

STRATIGRAPHICAL RANGE. Oxfordian—exact horizons not known.

TYPE SPECIMEN. A type specimen is not selected as this would have to be chosen from Orbigny's specimens of *Hemithiris spinulosa* (discussed below) and these are neither stratigraphically nor geographically accurately located.

MATERIAL. 2 specimens, collection of University of Dijon from Mt. Saon (Haute Marne) France; 6 specimens, collection of B.M.(N.H.) nos. B. 70044-49, from Haute Marne; 2 specimens Orbigny collection.

DESCRIPTION. *External characters.* The shell is equally biconvex and the width is greater than the length. The thin test is evenly covered with fine bifurcating ribs bearing numerous spine bases along their crests. The ribs are coarser and the spine bases more widely spaced than in *A. (Acanthorhynchia) panacanthina*.

Beak ridges are developed and limit the small but distinct interarea; the small, incurved beak is adpressed to the brachial valve and obscures the delthyrium. Deltidial plates are disjunct and only weakly developed; they appear briefly in a few of the anterior serial sections. Weakly developed growth lamellae, but not growth lines, may be present.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.30 cm	1.40 cm	2.54 cm
2.05 cm	1.10 cm	2.35 cm

Internal characters. *Pedicle valve.* Dental lamellae are completely lacking and the teeth are inserted laterally at a rather shallow angle.

Brachial valve. The most distinctive internal feature is the presence of what appears to be a cardinal process, developed from the inner hinge plates. The long, straight sockets, as seen in section 1.9 of text-fig. 25 appear to be distinctive. The crura are radulifer and curve slightly towards the pedicle valve. The median septum is poorly developed and is present only as a median ridge for most of its length.

DISTRIBUTION. The only records are from the Haute Marne area of France and from the Ledonien Jura.

REMARKS. The name *spinulosa* was first used by Oppel (1857) when he cited it as a "new name" for *Hemithiris senticosa* Orbigny in a list of Oxfordian fossils; unfortunately, he did not figure or state exactly what he meant by it.

Rollier (1917) suggested that the name *spinulosa* had been used by previous authors for two quite distinct species; one of which he considered to be "Argovien"

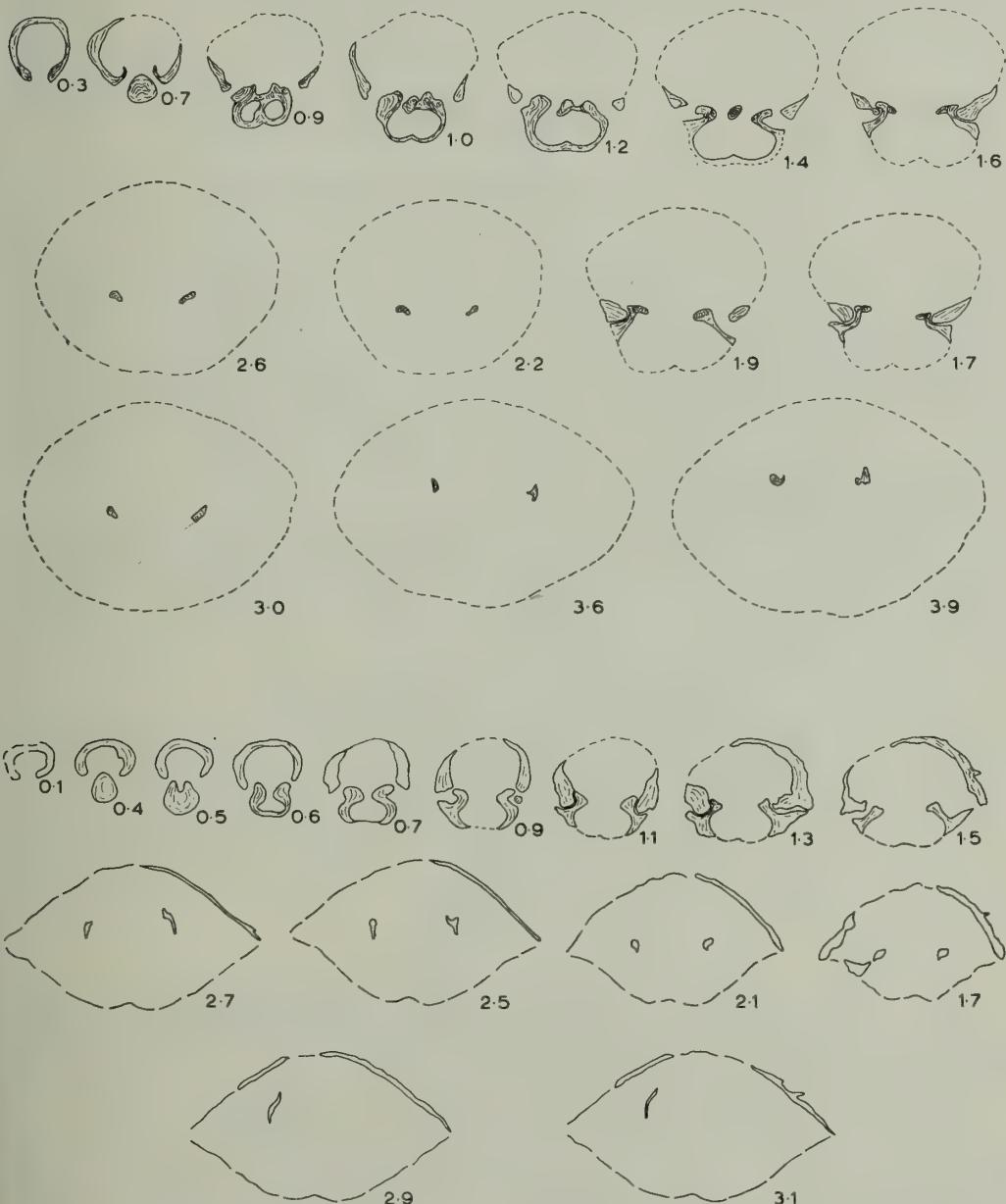


FIG. 25. TOP. Transverse serial sections of *A. (Acanthorhynchia) spinulosa* (Oppel). Oxfordian. Mont Saon, (Haute Marne), France. Specimen donated by the University of Dijon. ($\times 4$). BOTTOM. Transverse serial sections of *A. (Acanthorhynchia) sp.* Kimmeridgian. Oignon Limestone, (Ager & Evamy, 1963), Colomieu (Ain), France. ($\times 4$).

and the other "Oxfordien" in age. To remedy this he proposed that the name *spinulosa* be restricted to the larger, oval species from the "Argovien" and that the smaller, pyriform species of the "Oxfordien moyen et supérieur" be designated *Acanthothyris lorioli* sp. nov. Rollier's reason for preferring to restrict the name *spinulosa* to the larger form was that he considered Oppel's original designation inadequate and that, of the two species in question, this seemed to him to be the more likely to have been known to Orbigny, judging from the localities cited in the "Prodrome".

Plaster casts of the specimens labelled *Hemithiris senticosa* in the Orbigny collection at the Jardin des Plantes, Paris, were kindly made available to the author by the curator, Dr. Fischer. These specimens are in two boxes labelled 3782, containing three specimens from Chatel Censoir (Yonne) and 3782a, containing two specimens from Nantua (Ain). Both of the collection numbers contain a specimen of both *A. (Echinirhynchia) lorioli* and *A. (Acanthorhynchia) spinulosa* sensu Rollier. None of the specimens is referable to *A. senticosa* (Schlotheim). One of the specimens labelled 3782 probably belongs to a third, undescribed species and closely resembles a form collected by Dr. Evamy from the southern French Jura of Ain. Unfortunately not enough specimens of this form have been collected to make a full taxonomic investigation possible.

From the investigation of the original Orbigny material, described above, it seems that neither Oppel nor Rollier realised the diversity of specimens included by Orbigny under the name *Hemithiris senticosa*. However, the author would agree with Rollier's conclusions and these are here followed.

A. (*Acanthorhynchia*) *vilsensis* sp. n.
(Pl. 6, figs. 10-12, text-fig. 26 (bottom))

1886 *Rhynchonella myriacantha* Deslongchamps; Rothpletz: 156, pl. 12, figs. 24-27.

NAME. From the type area of the "Vilser Alp" in the Tirol.

DIAGNOSIS. Medium sized *Acanthorhynchia* with rather coarse ribbing ; beak suberect ; uniplication in anterior commissure.

STRATIGRAPHICAL RANGE. Given by Rothpletz as Callovian—*macrocephalus* to *lamberti* zones.

TYPE SPECIMEN. The holotype designated is the specimen figured by Rothpletz (1886) pl. 12, fig. 25, which came from Legam bei Vils in the Tirol ; this specimen is now in the Bayerische Staatsammung für Paläontologie und historische Geologie in Munich, and is numbered AS xiv 2.

MATERIAL. 17 specimens from the Bayerische Staatsammung.

DESCRIPTION. *External characters.* The adult specimens are biconvex, transversely oval in outline and with the width always greater than the length, while the juvenile forms have a subcircular outline. The beak is suberect ; beak ridges and interarea are only very weakly developed. In nearly all the specimens examined, the beak had been broken off about level with the top of the brachial valve. In a few more complete specimens, the delthyrium appears to be open but this feature

has not been satisfactorily observed. The test is evenly covered with bifurcating, spine-bearing ribs which are quite coarse, as compared with other species in the genus. A few growth lamellae are frequently present but growth lines have only been observed on one specimen. The anterior commissure has a characteristic low uniplication.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·70 cm	1·00 cm	2·00 cm
1·53 cm	0·93 cm	1·67 cm
1·33 cm	0·70 cm	1·43 cm

Internal characters. The specimen sectioned, which appeared to be of typical preservation for the locality, was very badly recrystallized and with the shell almost completely missing. The effect of this has been to obliterate the fine structure together with the crura which were rapidly lost in a mosaic of crystalline calcite ; the predominant lack of fine external ornament may also be a result of the poor preservation.

Pedicle valve. Slender, slightly diverging dental lamellae are present and bound a subquadrate delthyrial cavity. The teeth are large with distinctly flattened bases.

Brachial valve. The socket floors are very unusual in that they come to lie in a position sub-parallel to the plane of articulation. Both inner and outer socket ridges are well developed.

DISTRIBUTION. The species is only recorded from the type locality.

OCCURRENCE. In his original remarks, Rothpletz described it as occurring fairly abundantly in a "Brachiopoden-Lumachelle" together with numerous molluscs.

REMARKS. The species differs from *A. myriacantha*, as figured by Deslongchamps (1859), in being larger, having a uniplication in the anterior commissure and in having much coarser ribs on which the spine bases are more sparsely distributed. The small disjunct deltoidal plates figured by Deslongchamps have not been observed in *A. (Acanthorhynchia) vilsensis*.

A. (Acanthorhynchia) sp.

(Pl. 7, figs. 10–11, text-fig. 25 (bottom))

MATERIAL. 4 specimens including B.M. BB.44168, BB.44169.

REMARKS. The material was collected from the thin bedded Oignon Limestone* (Ager and Evamy, 1963) near Colomieu (Ain). Both externally and internally, the species shows considerable resemblance to *A. (Acanthorhynchia) spinulosa* ; however, the difference in stratigraphical horizon and the variability shown by the limited material available suggests that the species should be regarded as being derived from the former rather than conspecific with it. The largest specimen collected resembles one of the forms in the Orbigny Collection labelled *Hemithiris senticosa*.

* Oignon Limestone is of Upper Kimmeridgian age.

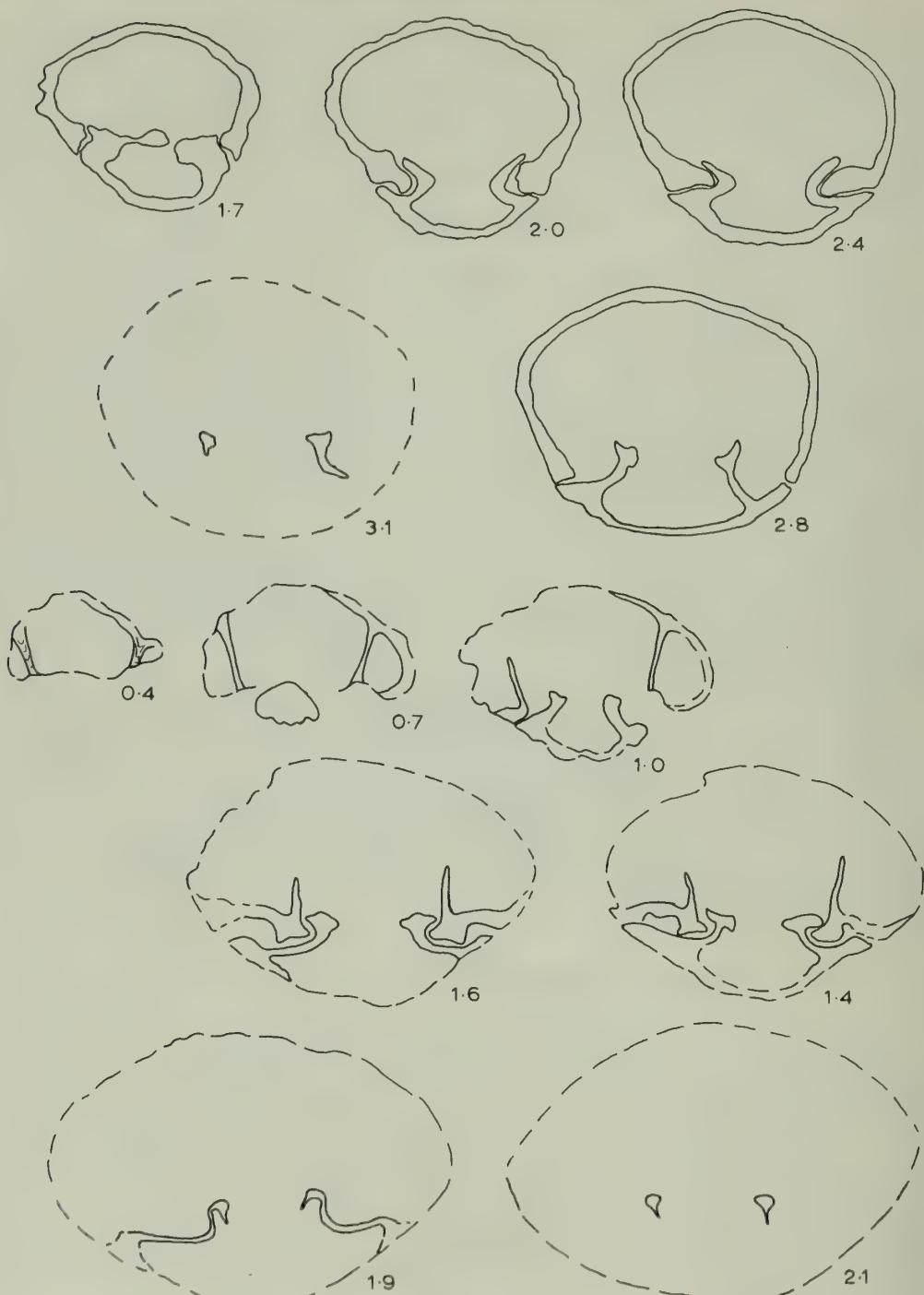


FIG. 26. TOP. Transverse serial sections of *A. (Echinirhynchia) senticosa* (Schlotheim). "Malm delta". Heiligenstadt, Germany. Specimen donated by the University of Erlangen. ($\times 8$). BOTTOM. Transverse serial sections of *A. (Acanthorhynchia) vilsensis* sp. nov. Topotype. Callovian. Legam bei Vils in the Tirol. Specimen donated by the Bayerische Staatsammlung. ($\times 8$).

ECHINIRHYNCHIA subgen. nov.

NAME. Latin *echinus-im*, the sea urchin : the shell of *Echinirhynchia* is covered with spines.

TYPE SPECIES. *Terebratulites senticosus* Schlotheim (1820).

DIAGNOSIS. Small to medium sized species of *Acanthorhynchia* ; usually subtriangular in outline ; valves equally biconvex or with a flattened brachial and more inflated pedicle valve ; beak small and either adpressed to the brachial valve or suberect ; deltoidal plates reduced or absent ; when the beak is suberect there is an open triangular delthyrium ; no dental lamellae or septalium ; anterior commissure rectimarginate.

STRATIGRAPHICAL RANGE. Oxfordian to Lower Volgian : *mariae*—*Gravesia* zones.

DISTRIBUTION. The subgenus appears, from the literature, to be restricted to the Jura, ranging from the southern French Jura through Switzerland to the Franconian Alb north of Erlangen ; the only records outside this area are of *A. (Echinirhynchia) fileyensis* (Buckman & Walker) from the Lower Calcareous Grit of Filey Brigg, Yorkshire, and of "*Acanthorhynchia* aff. *senticosa* (Schlotheim)" from Rumania (Patrulius, 1964).

REMARKS. The three species included are the only ones of which sufficient material has been obtained to allow description. Several nominal species, such as *Terebratula senticosa impressae* Quenstedt and *T. senticosa y alba* Quenstedt, almost certainly belong within the subgenus but the author has not been able to evaluate their position. The Quenstedt species mentioned above are the only ones recorded from the Swabian Alb area, although some of Oppel's records of *Rhynchonella spinulosa* probably included material referable to *Echinirhynchia*.

A. (*Echinirhynchia*) *senticosa* (Schlotheim)

(Pl. 7, figs. 1–3, text-fig. 26 (top))

- 1820 *Terebratulites senticosus* Schlotheim: 268.
- 1834 *Terebratula senticosa* Buch: 59–60.
- 1838 *Terebratula senticosa* Buch: 162–63, pl. 16, fig. 5.
- 1858 *Terebratula senticosa* Quenstedt: 457.
- 1871 *Terebratula senticosa silicea* Quenstedt: 115, pl. 39, fig. 66.
- 1886 *Rhynchonella senticosa* (Schlotheim); Rothpletz: 93, 156–57, pl. 15, figs. 4–9.
- 1889 *Acanthothyris senticosa* (Schlotheim); Buckman and Walker, 55–56.
- 1917 *Acanthothyris senticosa* (Schlotheim); Rollier: 80.
- 1918 *Acanthorhynchia senticosa* (Buch); Buckman, 70.

EMENDED DIAGNOSIS. Small to medium sized, pyriform *Echinirhynchia* ; test covered with numerous fine, spinose ribs ; beak relatively large and suberect to erect ; deltoidal plates absent resulting in an open triangular delthyrium ; rectimarginate.

STRATIGRAPHICAL RANGE. Kimmeridgian—Lower Volgian : *pseudomutabilis* to *Gravesia* zones.

TYPE SPECIMEN. Neotype (pl. 7, fig. 1), here designated, is the specimen figured by Rothpletz (1886) pl. 15, fig. 5, which is No. AS vii 330 in the collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie in Munich. It is considered desirable to designate a neotype as the name *senticosa* has been used very loosely in the past for widely differing forms.

MATERIAL. 12 specimens from the collection of the University of Erlangen; 11 specimens from the Bayerische Staatsammlung, Munich.

DESCRIPTION. *External characters.* The following is a translation of the original description by Schlotheim, "Partly in very complete examples, with perfectly preserved shells, from Grumbach, near Amberg, in the Pfalz, petrified in chert and probably belonging to the Jura formation. This very rare and remarkable Terebratulite, only recently discovered, has a somewhat elliptical, almost pear-shaped form, it is not particularly thick, is regularly convex with a fine, evenly striated, shagreen like surface and on both valves the somewhat prominent rays are covered with numerous, small sharp spines, by which this and *spinosa* may be distinguished from all other known species. It is very seldom found".

The Schlotheim description is quite accurate and mentions the two most distinctive characters, namely the pyriform shape and the fine, spine-covered ribs. The ribs characteristically bifurcate laterally thereby maintaining an even distribution over the surface. The species is also characterized by the possession of a rectimarginate anterior commissure. The beak is suberect and does not obscure the triangular delthyrial opening; no deltoidal plates have been observed. Beak ridges and inter-area are not developed. Some specimens have a few growth lamellae developed, but growth lines are not present; it is possible that the latter may have been obliterated as a result of the silicification suffered by all the specimens examined. The valves are about equally biconvex, although the brachial valve tends to be rather flat and may be the less inflated.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·35 cm	0·61 cm	1·17 cm
1·94 cm	0·87 cm	1·62 cm
1·35 cm	0·67 cm	1·22 cm

The last set of figures are the dimensions of the neotype.

Internal characters. The specimen sectioned was from Heiligenstadt, Franconia, and had a silicified shell and dolomitised infilling. This preservation has resulted in the loss of all fine detail and it has only been possible to give rather generalized drawings of the internal structures.

Pedicle valve. There are no dental lamellae and the large teeth are inserted laterally at a shallow angle.

Brachial valve. A cardinal process is present. Inner and outer socket ridges are both well developed. The form of the crura could not be determined as they disappeared into the recrystallized matrix immediately below the last section shown in text-fig. 26—top.

DISTRIBUTION. The Franconian and Swabian Jura.

OCCURRENCE. Dr. Zeiss, of Erlangen, has stated (personal communication 1965) that the material from Heiligenstadt occurs in the "Schwammfacies". There is no information available concerning the material figured by Rothpletz (1886).

REMARKS. The species, as remarked by Schlotheim, is rare and this has probably been the cause of the confusion about which species the name *senticosa* should be applied to. However, the silicified specimens figured by Rothpletz from the original locality cited by Schlotheim seem to fit the latter's description so exactly that there seems no doubt that this was the species intended by him. As can be seen from the original description, no exact geological horizon was given and some of the difficulty has undoubtedly arisen through Buch (1838) citing the Schlotheim locality for his *Terebratula senticosa* and stating the horizon for this locality to be "Dans les couches jurassiques inférieures, au-dessus du Lias". This statement seems to have lead several authors to reject the name *senticosa* when describing Upper Jurassic forms as they assumed Schlotheim's species was from the Middle Jurassic. However, Rothpletz gives the topotype material as being "Malm epsilon" in age and this agrees with the age given by Quenstedt (1871) for his *Terebratula senticosa silicea* from Sirchingen, while the material from Heiligenstadt in the collection of University of Erlangen is from the "Malm delta".

A. (*Echinirhynchia*) *lorioli* (Roller)
(Pl. 7, figs. 7-9, text-fig. 27)

- 1850 *Hemithiris senticosa* (pars) Orbigny: 375.
- 1857 *Rhynchonella spinulosa* (pars) Oppel: 608.
- 1871 ?*Terebratula y alba* Quenstedt: 114, pl. 39, figs. 63-65.
- 1897 *Acanthothyris spinulosa* (Oppel); Loriol: 146, pl. 17, fig. 17.
- 1904 *Acanthothyris spinulosa* (Oppel); Loriol: 284-85, pl. 27, fig. 45.
- 1917 *Acanthothyris Lorioli* Rollier: 79.
- 1917 ?*Acanthothyris dealbata* Rollier: 80.

EMENDED DIAGNOSIS. Medium sized, pyriform or sub-circular *Echinirhynchia*. Biconvex; rectimarginate; beak adpressed to the brachial valve.

STRATIGRAPHICAL RANGE. Oxfordian—the only exact records are from the *transversarium* zone.

TYPE SPECIMEN. Lectotype, here selected, the original specimen figured by Loriol (1897) pl. 17, fig. 17, collected from Montfaucon (Jura bernois).

MATERIAL. 7 specimens from the collection of the B.M.(N.H.) two, BB.44166, BB.44167, from the Jura; 10 specimens collected by Dr. Enay from the central French Jura; 2 specimens collected by Dr. Evamy from Ain.

DESCRIPTION. *External characters.* The species is normally biconvex but some specimens show a flattened brachial valve. The test is covered with many fine, bifurcating ribs bearing numerous fine spines. The beak is small and closely pressed to the brachial valve, obscuring the delthyrium; beak ridges and interarea not developed. Growth lamellae are sometimes present but growth lines have not been observed.

DIMENSIONS OF FIGURED SPECIMEN.

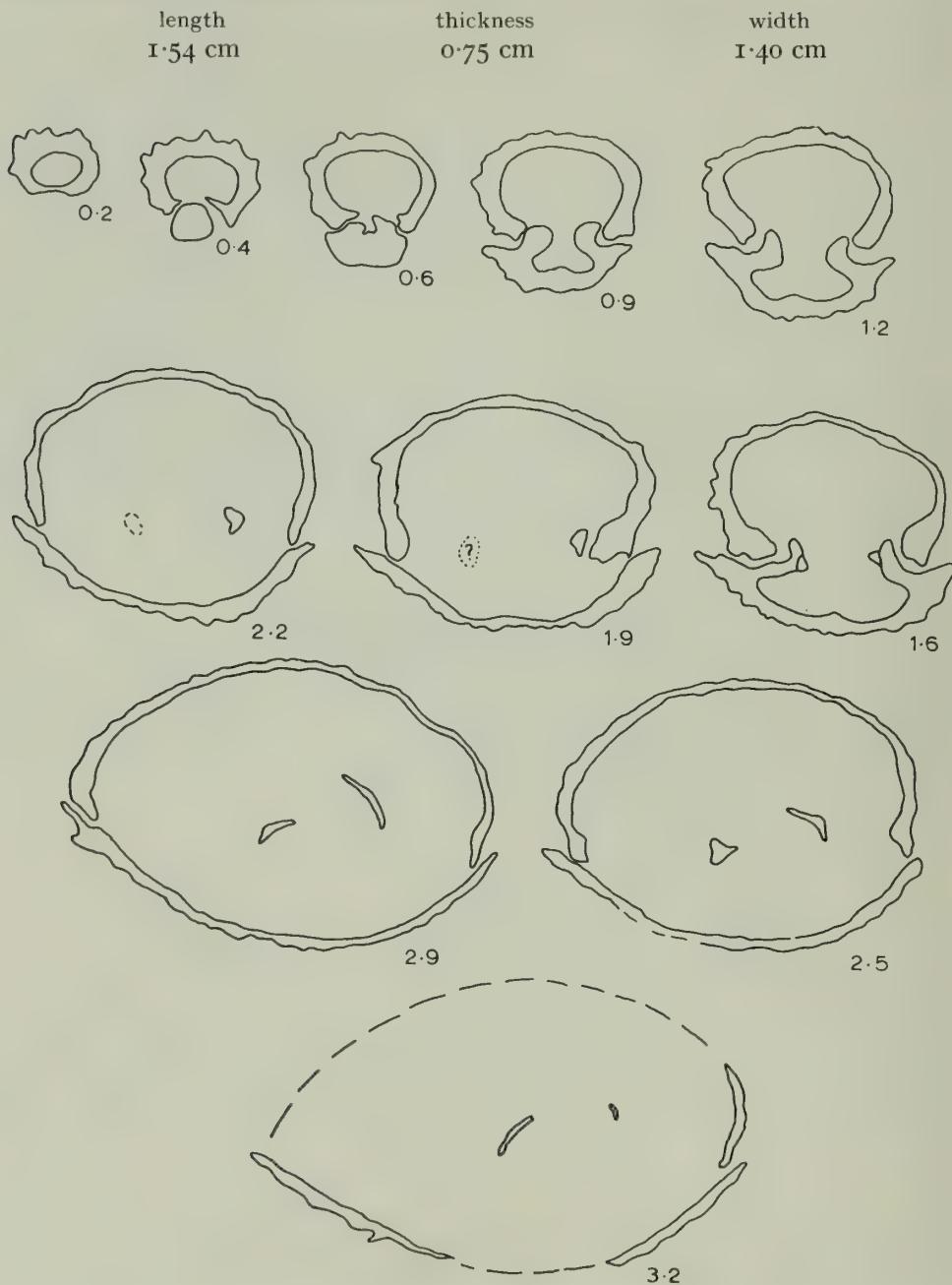


FIG. 27. Transverse serial sections of *A. (Echinirhynchia) lorioli* (Rollier). Oxfordian—*transversarium* zone. St. Sorlin, Liefnans (Jura), France. ($\times 8$).

Internal characters. *Pedicle valve.* There are no dental lamellae. The deltidial plates are disjunct and only weakly developed. The teeth are strong and inserted laterally at a rather shallow angle.

Brachial valve. A cardinal process is not present but the species exhibits the thickened inner hinge plates characteristic of the genus. The crura were not well preserved but are possibly of the calcarifer type. A median septum is only present as a low ridge.

DISTRIBUTION. The species has only been definitely recorded from the central and southern French Jura.

OCCURRENCE. The material collected by Dr. Enay was obtained from dark-coloured clays where it was associated with *Monticlarella triloboides*.

REMARKS. The specimen sectioned came from St. Sorlin (Jura) one of the localities mentioned by Rollier in his original description.

The separation of *A. (Echinirhynchia) lorioli* from *A. (Acanthorhynchia) spinulosa* is described under the latter.

A. (*Echinirhynchia*) *fileyensis* (Buckman & Walker)

(Pl. 7, figs. 4-6)

1889 *Acanthothyris senticosa* var. *fileyensis* Buckman and Walker: p. 56.

EMENDED DIAGNOSIS. Small to medium sized *Echinirhynchia*; beak small and suberect to erect; valves equally biconvex.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* and lower *cordatum* zones.

TYPE SPECIMEN. Lectotype, here selected, specimen no. B. 31867 in the Walker Collection of the B.M.(N.H.), collected from the Lower Calcareous Grit of Filey, Yorkshire.

MATERIAL. 6 specimens from the Walker Collection in the B.M.(N.H.); nos. B. 31313, B. 31335, B. 31275; 2 specimens from the collection of the Naturhistorisches Museum, Basel.

DESCRIPTION. *External characters.* The shell is biconvex and pyriform in outline with a straight anterior margin. The ribs are fine but well marked and covered with spine bases. The beak is small and erect or sub-erect; beak ridges and interarea are not developed. Details of deltidial plates, if any, and delthyrium not observed.

DIMENSIONS OF FIGURED SPECIMEN. The following measurements are those of the lectotype.

length	thickness	width
0·80 cm	0·37 cm	0·74 cm

Internal characters. Not investigated through lack of material.

DISTRIBUTION AND OCCURRENCE. The species has only been definitely recorded from Filey, Yorkshire, where it occurs in the Lower Calcareous Grit. The only other possible conspecific material known to the author is two specimens from the "Renggeri-Thon" of Baden, in the collection of the Naturhistorisches Museum, Basel and numbered L 1701/1-2.

REMARKS. The form was first mentioned by Buckman and Walker in 1889 in their discussion of the spinose Rhynchonellidae, when they described it under the name of *Acanthothyris senticosa* var. *fileyensis* and suggested that it resembled *A. senticosa* of Orbigny. However, as *A. (Echinirhynchia) fileyensis* shows marked differences from both the specimens in the Orbigny Collection and *A. (Echinirhynchia) senticosa* (Schlotheim), it has been decided to describe it as separate species despite the paucity of material.

Subfamily **TETRARHYNCHIINAE** Ager, 1965*b*
Genus **SOMALIRHYNCHIA** Weir

- 1925 *Somalirhynchia* Weir: 79.
- 1929 *Somalirhynchia* Weir; Weir: 38–39.
- 1935 *Somalirhynchia* Weir; Muir-Wood: 93.
- 1964 *Praecyclothyris* Makridin, 150–51.
- 1965*b* *Somalirhynchia* Weir; Ager: H614.

TYPE SPECIES. *S. africana* Weir, by original designation.

EMENDED DIAGNOSIS. Large, subpentagonal, trilobate rhynchonellids; 20–30 coarse, simple, subangular ribs; large, sub-erect beak; possesses septalial plates and median septum, which together form a septalium; crura radulifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian—Lower Kimmeridgian.

DISTRIBUTION. Somaliland, Syria, N.W. Europe, Russia.

REMARKS. Weir (1925, 1929) gave the name *S. africana* to the species figured by Noetling (1886) as *Rhynchonella moravica* Uhlig; he suggested that the differences in outline and particularly in muscle scar patterns necessitated regarding *R. moravica* Noetling as differing from *R. moravica* Uhlig not only specifically but generically. The author considers that Weir was probably correct in establishing a new species for Noetling's *R. moravica*. However, in internal structure, as well as general external appearance, *S. africana*, in the author's opinion, closely resembles *R. moravica* Uhlig and should be regarded as congeneric with it.

In basing his taxonomy almost entirely on the muscle scar patterns, Weir was closely following the ideas of Buckman. However, it is now considered that the similarity exhibited by all the other features outweigh in taxonomic significance the dissimilarity of the muscle patterns. The internal details of *R. moravica* Uhlig were figured by Wiśniewska (1932) and, allowing for the differences in appearance caused by her angle of sectioning, are closely comparable to those given by Muir-Wood (1935) for *S. africana*. They appear to have little in common with *Septaliphoria arduennensis* (Oppel), the type species of *Septaliphoria* Leidhold, to which genus *R. moravica* Uhlig was assigned by Wiśniewska. Consequently, the author does not understand on what grounds Muir-Wood (1935) remarked, "Further study of the internal characters of *R. moravica* by Wiśniewska (1932, p. 22) has emphasized the differences between the two species (i.e. *R. moravica* Uhlig and *S. africana* Weir). *R. moravica* is now assigned to the genus *Septaliphoria* (Leidhold 1920)".

The wide geographical distribution of the genus is coupled with a very limited stratigraphical range. It is considered that the distribution of the genus can be

extended to Russia, as it appears from Makridin's figures that some at least of his species of the genus *Praecyclothyris* should be attributed to *Somalirhynchia*. That the genus has not previously been recorded from Europe is probably the result of its name, which has possibly been taken by previous authors as implying a restricted geographical occurrence.

***Somalirhynchia sutherlandi* (Davidson)**

(Pl. 7, figs. 12–16, text-fig. 29)

- 1873 *Rhynchonella Sutherlandi* Davidson: 196, pl. 8, figs. 1–2.
- 1878 *Rhynchonella Sutherlandi* Davidson; Davidson: 190–91, pl. 25, figs. 5–8.
- 1917 *Rhynchonella Sutherlandiae* Davidson; Rollier: 172.
- 1918 *Rhynchonella Sutherlandi* Davidson; Buckman: 51.

EMENDED DIAGNOSIS. Medium to large sized *Somalirhynchia*; 15–25 coarse, simple, angular ribs; usually trilobate; suberect beak, septalium present; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—probably restricted to the upper *mutabilis* and *pseudomutabilis* zones.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Davidson (1878), pl. 25, fig. 5).

MATERIAL. 19 specimens from the collection of the Geological Survey of Scotland, together with the very limited material available at the B.M.(N.H.) nos. B. 29749, B. 29752, B. 22586, B. 29751, B. 29753. A recent attempt by the author to collect further material yielded a single fragmentary specimen.

DESCRIPTION. *External characters.* The species is distinctive on account of the very large size attained by many individuals; Davidson (1878) claimed it to be the largest Mesozoic rhynchonellid. The outline is subpentagonal and the shell is biconvex with the brachial valve the more inflated. It is generally trilobate but a few specimens have been observed displaying quite marked asymmetry. Width, according to Davidson, is always greater than length, and while this seems to be correct the crushed nature of much of the material makes this difficult to ascertain in more than a few cases. Plate 7 figures the best preserved material available.

The strong, suberect beak is flanked by well defined beak ridges which limit the incurved interarea. A relatively small pedicle opening is present; the deltidial plates, as seen in transverse section, are strongly conjunct. Fine, concentric growth lines have been observed on one specimen; this may well reflect the poor preservation rather than the genuine lack of such ornament on most specimens.

DIMENSIONS OF FIGURED SPECIMEN.

length	thickness	width
2·67 cm	2·33 cm	3·16 cm

Internal characters. The specimen sectioned was slightly crushed, resulting in dorso-ventral flattening of the shell. The outline of some of the internal features was partly distorted by pressure solution caused by the coarse, quartz matrix.

Pedicle valve. A pedicle collar is present; the deltidial plates are conjunct and "crumple up" against one another. A quadrate delthyrial cavity is flanked by

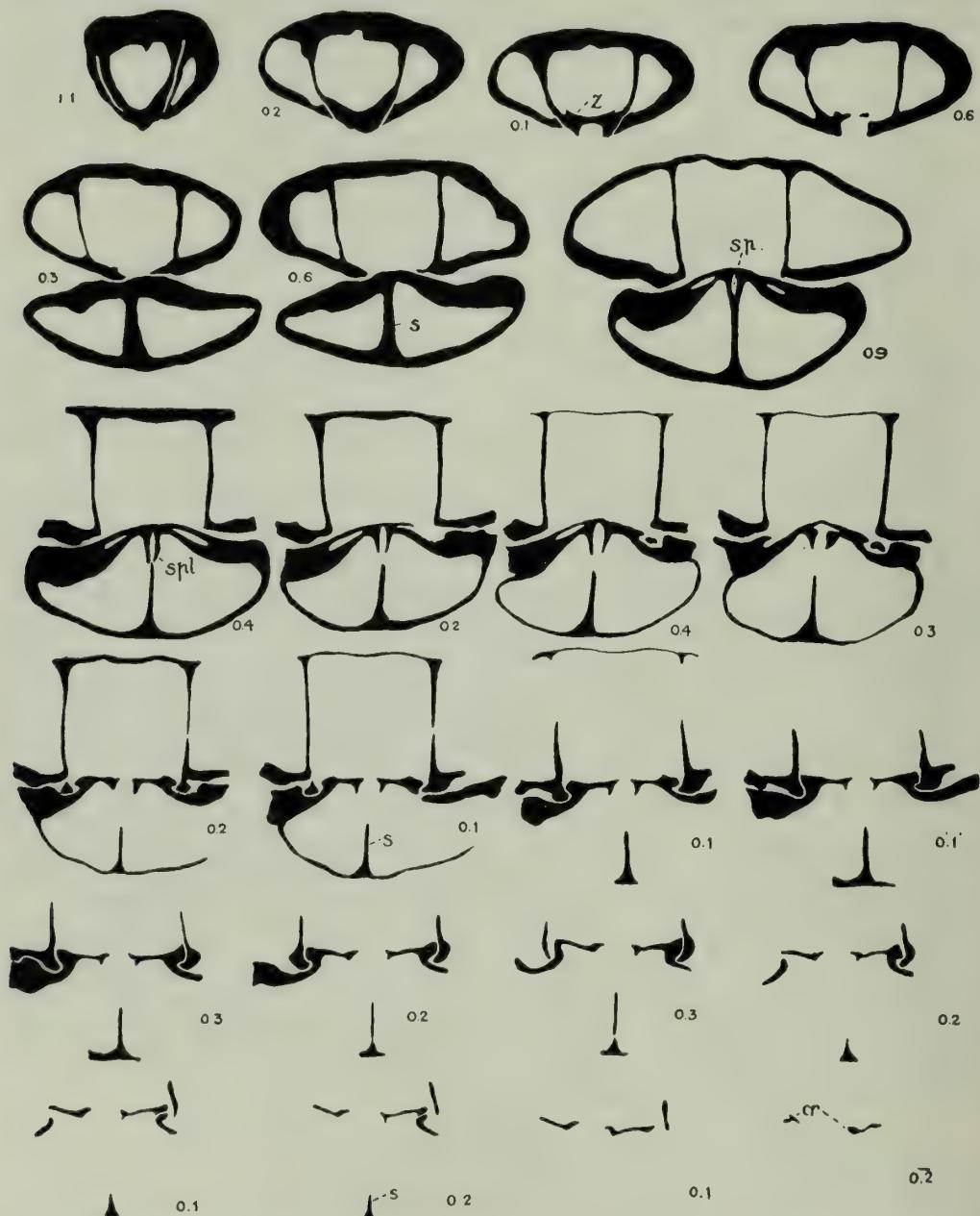


FIG. 28. Transverse serial sections of *Somalirhynchia africana* Weir. Taken from Muir-Wood (1935, fig. 8, p. 95).

long, stout, subparallel dental lamellae. The hinge apparatus is strongly developed with massive crenulated teeth and strong lateral denticulae.

Brachial valve. The most obvious feature is the presence of a median septum and well developed septalial plates forming a septalium. The crural bases do not become apparent, as seen in transverse section, until after the hinge plates have divided and the septalial plates disappeared. The crura are radulifer. The sockets are crenulated and both the inner and outer socket ridges are strongly developed.

DISTRIBUTION. The species has only been recorded from the Helmsdale area of Sutherland, Scotland.

OCCURRENCE. The only known occurrence is in the Kimmeridgian "Boulder Beds" of the Helmsdale area, east Sutherland, Scotland. Bailey and Weir (1935) suggested that the rhynchonellids, together with the terebratulids and corals, owed their presence in these beds to the effects of submarine faulting. They suggested a near-shore fault scarp which, "separated a comparatively shallow-water facies, characterized by rounded pebbles, sand, *Rhynchonella*, *Terebratula*, *Ostrea*, sea urchins corals, etc. from a comparatively deepwater facies, characterized by mud, debris of land plants, ammonites etc.". The rhynchonellids etc. were then swept over the scarp edge by the movements of the fault and the accompanying tsunamis.

Ager (1965a), accepting this hypothesis, suggested that the *S. sutherlandi* inhabited, "sublittoral, non-depositional sea floors"; the rarity of the species then being accounted for by the infrequency with which such deposits are preserved. However, although no other representative of the genus occurs in Britain, *S. moeschi* (Haas) is present in the "Rauracian" of the French and Swiss Jura. Material of the latter species has been given to the author by Dr. Enay of the University of Lyon and he has stated (personal communication, 1965), that *S. moeschi*, at least within the Jura meridionale, always occurs in association with corals. From this it would also seem possible that *S. sutherlandi* inhabited shallow marine environments and was not necessarily restricted to rocky shores. The presence of corals at Helmsdale indicates the possibility of a reef environment being available.

REMARKS. It appears that *S. sutherlandi* has not been further described since Davidson in 1878 and during this time there have been only two tentative generic assignations. In the first, Buckman (1918), placed it in his genus *Rhactorhynchia* but although he indicated his uncertainty he did not discuss the matter. Ager (1965a), suggested the possibility of *sutherlandi* being in the genus *Russirhynchia* Buckman, which is otherwise restricted to the Russian Platform. The present author, however, prefers to attribute the species to the genus *Somalirhynchia* Weir. Reproduced below, text-figure 28, are the serial sections given by Muir-Wood (1935) for the type species, *S. africana* Weir, and it can be seen that they show a striking resemblance to those of *S. sutherlandi*. Externally the species are also comparable in general shape, ribbing, and form of the beak and the pedicle opening. Both internally and externally "*R.*" *sutherlandi* appears to be much closer to *S. africana* than to the type species of *Russirhynchia* namely, *R. fischeri* (Rouillier).

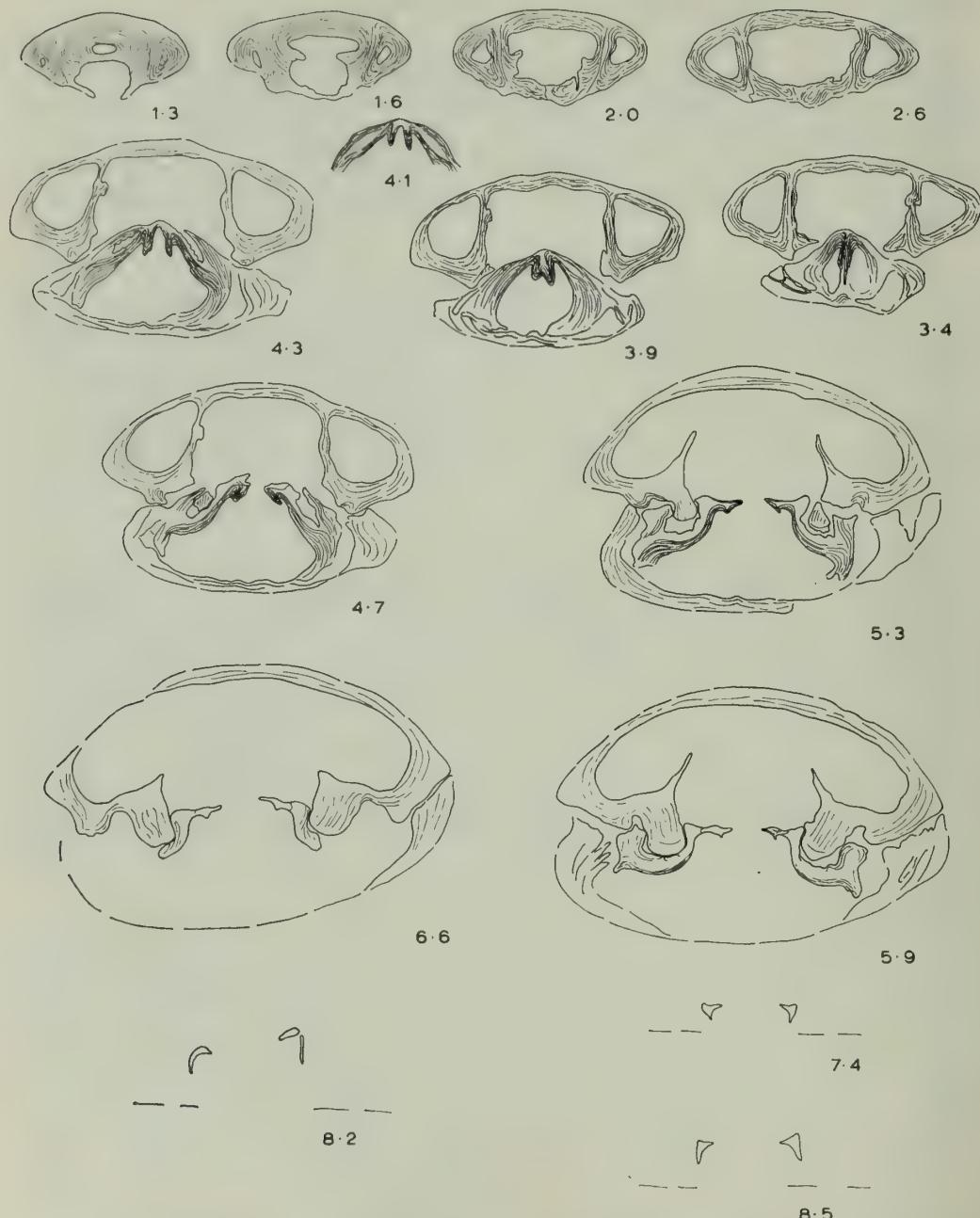


FIG. 29. Transverse serial sections of *Somalirhynchia sutherlandi* (Davidson). Topotype. Kimmeridgian. Boulder Beds. West Garty, Sutherland. Specimen donated by the Geological Survey, Edinburgh. ($\times 3$).

Somalirhynchia moeschi (Haas)

(Pl. 8, figs. 1-3, text-fig. 30)

- 1890 *Rhynchonella trilobata* Zieten var. *Möschi* Haas: 58-59, pl. 7, fig. 7, pl. 8, figs. 1-2.
 1893 *Rhynchonella trilobata* Zieten var. *Moeschi* Greppin: 98, pl. 7, figs. 3-4.
 1917 *Rhynchonella Moeschi* Rollier: 174.
 1932 ?*Septaliphoria moravica* (Uhlig); Wiśniewska: 22-24, pl. 5, figs. 3-4.
 1964 *Praecyclothyris moeschi* (Rollier); Makridin: 158-60, pl. 6, fig. 8, pl. 7, fig. 1.

EMENDED DIAGNOSIS. Medium to large, subpentagonal *Somalirhynchia*; markedly trilobate with about 6-8 ribs on the fold; septalium present although septalial plates relatively weakly developed; crura radulifer.

STRATIGRAPHICAL RANGE. Upper Oxfordian; records, such as those of Haas (1890), from the Kimmeridgian are almost certainly the result of misidentifying *Lacunosella trilobataeformis* Wiśniewska. The latter species strongly resembles *S. moeschi* externally but can be readily differentiated by its possession of bifurcating ribs.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Haas (1890) pl. 7, fig. 1; the specimen was obtained from the "Wangener Schichten" of "Engelberg bei Olten".

MATERIAL. 80 specimens collected by Dr. Enay from the "départements" of Jura and Ain. 6 specimens from the collection of the University of Dijon labelled, "Corallien inférieur?", 7 specimens collected by the author from Pontarlier, near Besançon.

DESCRIPTION. *External characters.* The species has a subpentagonal outline and is markedly trilobate. There are between 20 and 30 coarse, simple subangular ribs of which 6 to 8 lie on the fold.

The sharp, suberect beak is flanked by weak beak ridges and these in turn delimit the slightly incurved interarea. The deltidial plates, which tend to project slightly around the circular, submesothyridid pedicle opening, are conjunct; however, in many specimens the deltidial plates are missing, presumably through having fallen out after death, leaving an open delthyrium.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·57 cm	2·70 cm	3·82 cm
3·12 cm	2·18 cm	3·00 cm

Internal characters. *Pedicle valve.* The lateral cavities are small and limited by slender, subparallel, persistent dental lamellae. The delthyrial cavity is quadrate. The teeth are crenulated; lateral denticulae are only weakly developed.

Brachial valve. A septalium is present; although the median septum is quite strong and persistent, the septalial plates are only weakly developed. The radulifer crura have clearly differentiated crural bases. The hinge plates are arched ventrally.

DISTRIBUTION. The French and Swiss Jura; ? Poland.

OCCURRENCE. The specimens collected by the author came from a limestone with a typical reef fauna, namely lamellibranchs, terebratulids, gasteropods and

JURASSIC RHYNCHONELLIDS

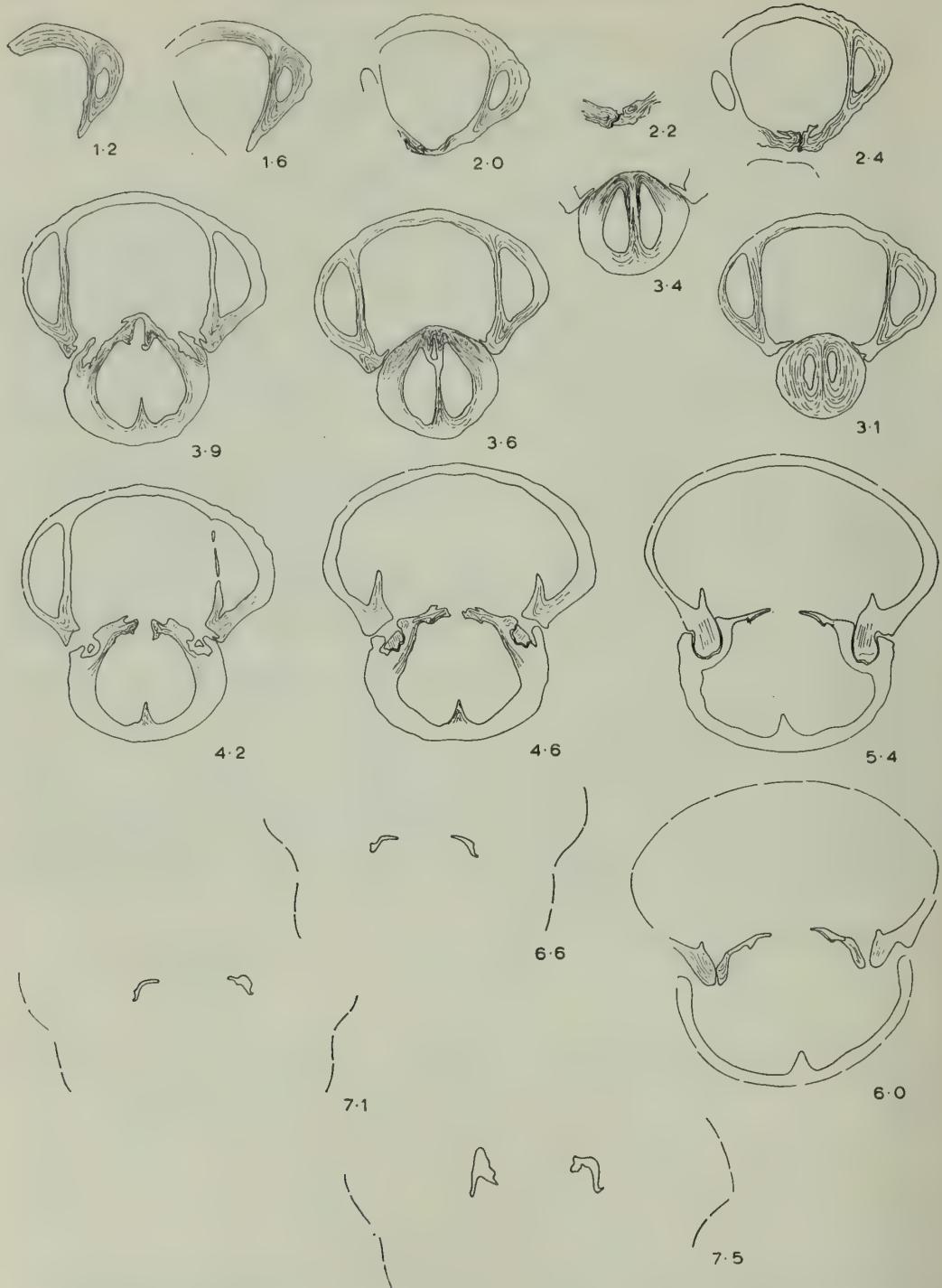


FIG. 30. Transverse serial sections of *Somalirhynchia moeschi* (Haas). Oxfordian—
transversarium zone. Arinthod (Jura). ($\times 3$).

echinoids together with numerous branching corals. *S. moeschi* was the most common brachiopod, followed in numbers by the smooth terebratulids, while the ribbed terebratulids were the rarest element of the fauna.

REMARKS. In discussing *Septaliphoria moravica* (Uhlig), Wiśniewska suggested that *Rhynchonella trilobata* var. *Möschi* was probably a synonym. Unfortunately, the author has not seen the original specimens of Uhlig, Haas or Wiśniewska. Judging from the published figures and assuming these to be typical, it would appear that the specimens described by Wiśniewska are conspecific with *S. moeschi* (Haas) and that "*Rhynchonella*" *moravica* Uhlig is probably a separate species, the latter being differentiated by its more trilobate form. However, "*R.*" *moravica*, which occurs in the *bimammatum* zone is almost certainly congeneric.

In 1964, Makridin divided *R. moeschi* Rollier into two subspecies, namely *moeschi moeschi* and *moeschi donetziana*. He then selected the latter as the type of his new genus *Praecyclothyris*; however, as under the international rules of nomenclature the type must be *moeschi moeschi*; it is suggested that *Praecyclothyris* is a synonym of *Somalirhynchia* Weir. As *Somalirhynchia* is not mentioned in the Russian "Treatise", it is assumed that the rather obscure publications in which it has been described are not known to palaeontologists in the Soviet Union.

Subfamily CYCLOTHYRIDINAE Makridin, 1955
Genus **SEPTALIPHORIA** Leidhold

- 1920 *Septaliphoria* Leidhold: 354–55.
- 1932 *Septaliphoria* Leidhold; Wiśniewska: 18–20.
- 1960 *Septaliphoria* Leidhold; Makridin: 251–52.
- 1964 *Septaliphoria* Leidhold; Makridin: 96–7.
- 1965b *Septaliphoria* Leidhold; Ager: H619.

TYPE SPECIES. *Rhynchonella arduennensis* Oppel, by original designation.

EMENDED DIAGNOSIS. Medium sized, subpentagonal rhynchonellids; 10–25 coarse, simple, subangular ribs; septulum present; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—?Kimmeridgian.

DESCRIPTION. *External characters.* The genus consists of ordinary looking uniplicate rhynchonellids, having a tendency towards asymmetrical development of the anterior commissure. The complete, bilobed asymmetry characteristic of *Torquirhynchia* is very rarely found and in most cases the asymmetry of the anterior commissure has resulted from displacement of the uniplication. *Septaliphoria* is biconvex with the brachial valve the more inflated; there is no posterior smooth area.

The well developed, suberect beak is flanked by beak ridges which limit an incurved interarea. A large, hypothyridid or submesothyridid pedicle opening is present; the deltoidal plates are usually, but not invariably, conjunct.

Internal characters. *Pedicle valve.* The dental lamellae are subparallel and relatively short. The teeth may be slightly crenulated; lateral denticulae are variably developed.

Brachial valve. The most important feature is the septalium ; in his original description Leidhold (1920) regarded this structure as the diagnostic feature of the genus.

The crural bases are clearly differentiated and are distinctive in that they can be seen at the same level as the septalial plates in transverse section. In both the species sectioned, the crura ended with the curiously shaped, but consistent, processes seen in text-figs. 31–33.

SPECIES. The following nominal species are attributed to the genus :

S. arduennensis (Oppel) (1858, pp. 615, 639, 654)

?*S. hudlestoni* (Rollier) (1917, p. 172)

S. paucicosta sp. nov.

S. pinguis (Roemer) (pars in Wiśniewska 1932, pp. 24–29, pl. I, figs. 1–18)

?*S. septentrionalis* sp. n.

?*S. pectunculoides* (Etallon) (in Makridin 1964, pp. 102–5, pl. I, figs. 4–6)

S. sobolevi Makridin (1964, pp. 97–99, pl. I, figs. 16–18).

DISTRIBUTION. The taxonomic confusion which has surrounded the genus, together with the lack of published serial sections, makes identification from the literature very difficult. However, the genus occurs in Yorkshire, northern France, the Swiss Jura and ?Dorset. Some of Makridin's species of *Septaliphoria* from the Russian Platform also undoubtedly belong to the genus, as here defined.

REMARKS. Much confusion has arisen about the exact nature of the genus, mainly as a result of two factors. Firstly, Leidhold (1920) chose as his type species the poorly defined *Rhynchonella arduennensis* of Oppel, and secondly, because Leidhold's description of the septalium was based on a misunderstanding regarding its development.

The synonymy of the type species is described under *S. arduennensis*. A full description, with figures and sections of the septalium has already been given in the section on morphology and it is only necessary to repeat here that it forms through the fusion of the septalial plates with the septum and not as a result of a bifurcation of the septum, as originally suggested by Leidhold.

***Septaliphoria arduennensis* (Oppel)**
(Pl. 8, figs. 4–5, text-figs. 31–32)

- 1858 *Rhynchonella Arduennensis* Oppel: 615, 639, 654.
- 1871 *Terebratula inconstans* Quenstedt: 141, pl. 40, fig. 57.
- 1917 *Rhynchonella Arduennensis* Oppel; Rollier: 171–72.
- 1920 *Septaliphoria arduennensis* (Oppel); Leidhold: 354, pl. 5, fig. 2.
- 1932 *Septaliphoria arduennensis* (Oppel); Wiśniewska: 18.

EMENDED DIAGNOSIS. Medium sized subpentagonal to subtriangular *Septaliphoria* ; biconvex ; frequently slightly asymmetrical ; about 20 simple, subangular ribs ; well developed septalium crura radulifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian ; *cordatum* and lower *transversarium* zones.

TYPE SPECIMEN. A neotype is here proposed in view of the uncertainty which has surrounded this important species. Although the specimen chosen is not from any of the localities cited by Oppel (1858) it is from the horizon mentioned by him, namely the "Terrain à Chailles", and has been selected to conform as nearly as possible to the specimen figured by Leidhold, as he was the first to figure the species as such and, consequently, his figure has been accepted as definitive both of the species and of the genus *Septaliphoria* of which it is the type. Unfortunately, it is not possible to collect material from the area around Mézières mentioned by Leidhold, as the Oxfordian is no longer exposed there (Dr. Maubeurge, personal communication 1965). As the specimen figured by Leidhold shows the internal structure, it seems probable that it was a silicified specimen from the "Terrain à Chailles".

The author has not been able to find the type specimens of either Oppel or Leidhold and it is considered highly unlikely that they still exist in a recognizable form. The neotype was collected from the "Terrain à Chailles" at Pagny-sur-Meuse, near Nancy, France.

DIMENSIONS OF NEOTYPE. Length 2·33 cm; thickness 1·90 cm and width 2·60 cm.

MATERIAL. 25 specimens from Pagny-sur-Meuse (Meurthe et Moselle), including BB.44173, BB.44174.

DESCRIPTION. *External characters.* The outline of adult specimens is subpentagonal while that of the smaller ones is subtriangular; the smaller specimens also tend to be equally biconvex while the larger ones have a more inflated brachial valve.

The beak is suberect and flanked by fairly well developed beak ridges. The inter-area is relatively large and either flattened or slightly incurved. The deltidial plates are either disjunct or just conjunct. A large, well developed, circular pedicle opening is present and was presumably functional at all stages. Concentric ornament appears to be restricted to occasional, poorly developed growth lamellae.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2·49 cm	1·73 cm	2·67 cm
2·33 cm	1·90 cm	2·60 cm

Internal characters. All the specimens available were silicified and much of the fine detail of the internal structure has been lost.

Pedicle valve. The narrow, elongated lateral cavities are delimited by slender, ventrally divergent dental lamellae which break away from the ventral wall of the valve well to the posterior of the plane of articulation. The teeth are strong and crenulated; lateral denticulae are present.

Brachial valve. A septalium is present and can be clearly seen in text-fig. 32. It is less distinct in the other specimen sectioned, probably as a result of partial silicification. The crural bases are distinct and can be seen lying immediately behind the septalial plates in section 1, 5 of text-fig. 31; the crura are of the radulifer type. The hinge apparatus is strong with crenulated sockets and both inner and outer socket ridges well developed.

DISTRIBUTION. The distribution of the species is very uncertain and the only definite records are from the "Terrain à Chailles", of northern France and the Swiss Jura around Basel.

OCCURRENCE. The specimens collected by the author at Pagny were from sandy limestones containing cherty bands and nodules. The large associated fauna consisted of ammonites, lamellibranchs, mainly *Pholadomya* and *Lima* types, and *Thurmannella obtita*. *T. obtita* was the most abundant element and tended to

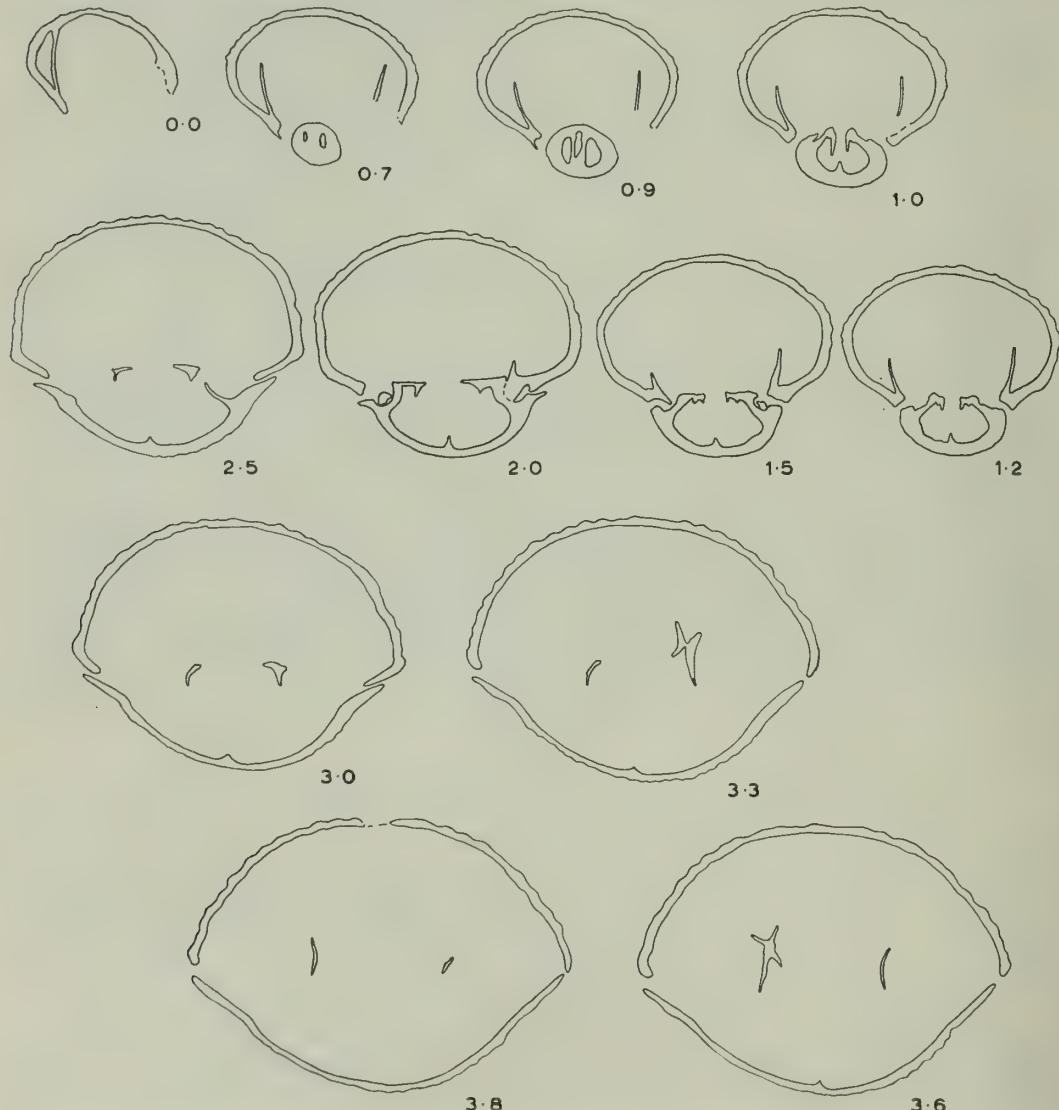


FIG. 31. Transverse serial sections of *Septaliophoria arduennensis* (Oppel). Oxfordian. "Terrain à Chailles". Pagny-sur-Meuse (Meurthe et Moselle). ($\times 3$).

occur in groups while *S. arduennensis* occurred as single specimens and was much less common.

REMARKS. The name *arduennensis* first appeared in the literature in 1858 when Oppel used it as a "n. sp." for, "*Rh. inconstans* d'Orb. 1848, Prodr. 13 460 (non Sow.)", in a list of Oxfordian fossils. He gave no description but subsequently included it in faunal lists from the ironstone of the Ardennes, as developed at Vieil-Saint Remy and Neuvizi, which he was describing together with other localities of his *Ammonites biarmatus* zone. However, he stated that he considered the above localities to be possibly of a higher horizon. Oppel's other citation of the species is from the "Zone des *Cidaris florigemma*. (Terr. à Chailles und unteres Coralrag)", of the Swiss Jura.

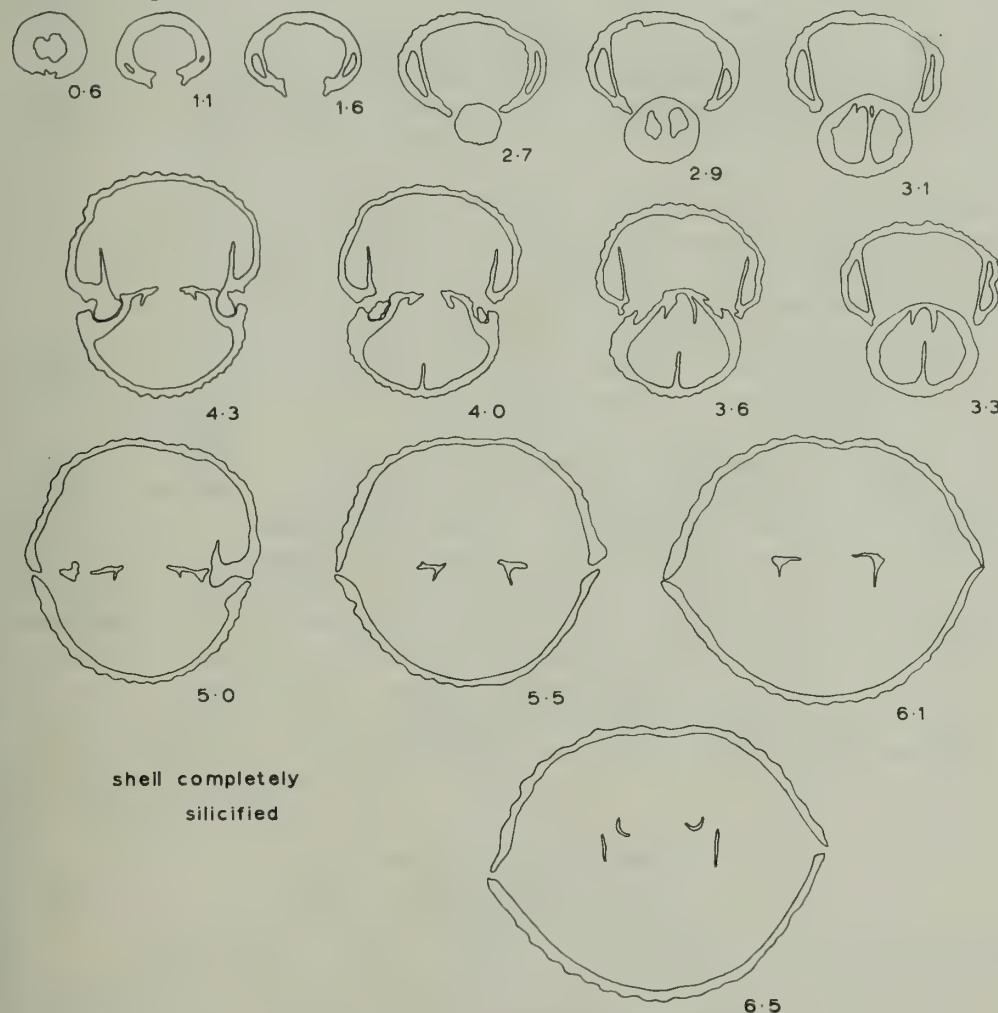


FIG. 32. Transverse serial sections of *Septaliphoria arduennensis* (Oppel). Oxfordian. "Terrain & Chailles". Pagny-sur-Meuse (Meurthe et Moselle), France. ($\times 3$).

Arkell (1956) thought the Neuvizy Ironstone to be of *cordatum* age, thus making it the lateral equivalent of the Terrain à Chailles which is *cordatum* and lower *transversarium* zones in age. This would then restrict *arduennensis*, as it was presumably conceived by Oppel, to those zones.

Oppel proposed a new name for Orbigny's *R. inconstans* as he realized that the Oxfordian species mentioned by Orbigny was not the one which had already been described by Sowerby (1821) under the name *inconstans* from the English Kimmeridgian. As Oppel was proposing *arduennensis* as a new name for *R. inconstans* of Orbigny, it seems reasonable to assume that the species to which he was referring exhibited some degree of asymmetry. Therefore, it seems fairly certain that by *arduennensis* he meant the medium sized asymmetrical rhynchonellid occurring quite frequently in the Lower Oxfordian of the areas mentioned by him. As can be seen from the figured specimens, the species shows varying degrees of asymmetry but is occasionally perfectly symmetrical. The latter condition is shown by the specimen figured by Leidhold and this again has lead to some confusion. The species does not appear to have been figured other than by Leidhold and as *Terebratula inconstans* (pars) by Quenstedt.

In making *arduennensis* the type species of his new genus *septaliphoria*, Leidhold gave no description and merely commented that it came from the "Oxford-Stufe". The caption to the one specimen figured described it as coming from the "Oxford-Stufe" of Mézières.

Rollier (1917) suggested the possibility of *R. arduennensis* Oppel being a synonym of *Terebratulites helveticus* of Schlotheim (1813). The latter species was figured by Schlotheim but not given any description other than being listed as occurring in the "Jurakalkstein" near Basel and being given the citation "Scheuchzer (1718), fig. 105". The latter figure is virtually indeterminable except as a ribbed brachiopod. Although Rollier maintained that *R. helvetica* "est incontestablement une forme asymmetrique de l'Oxfordian supér. et du Rauracien inférieur, très, fréquente dans le Jura aux environs de Bâle," this statement seems to be erring on the side of optimism in view of inadequacy of the figures and the lack of detail given by both Scheuchzer and Schlotheim. Quenstedt (1871) considered the Schlotheim species to be his *Terebratula lacunosa multiplicata* from the "Malm gamma"; this does not appear likely but at least demonstrates the uncertain nature of the species. It therefore seems best to treat *T. helvetica* Schlotheim as a nomen dubium.

The *Terebratula helvetica* Schlotheim figured by Zieten (1831) possibly belongs to the genus *Septaliphoria*, but it is not considered to be conspecific with *S. arduennensis*.

***Septaliphoria paucicosta* sp. n.**
(Pl. 9, figs. 5-6, text-fig. 33)

- 1878 *Rhynchonella lacunosa* (Schlotheim); Davidson: 196-97, pl. 16, figs. 13-14.
1917 *Rhynchonella helvetica* (Schlotheim); Rollier: 171.

NAME. Latin *paucus-a-um*, few; *costa-ae*, rib: the species has relatively few ribs.

DIAGNOSIS. Medium to large *Septaliphoria*; 9–15 very coarse subangular ribs; no smooth area posteriorly; uniplicate or asymmetrical; conjunct deltoidal plates; strong suberect beak; crura radulifer.

STRATIGRAPHICAL RANGE. Oxfordian—*mariae* and *cordatum* zone; the Lower Calcareous Grit of Yorkshire.

TYPE SPECIMEN. Holotype, BB. 45394, selected from a box of specimens in the collection of the B.M.(N.H.) with the locality given as “Hutton Bushell, Beedale, Yorkshire”.

DIMENSIONS OF HOLOTYPE. Length 2·61 cm, thickness 1·78 cm, width 2·90 cm.

MATERIAL. About 100 specimens, all from the collection of the B.M.(N.H.) B. 26924, B. 26903.

DESCRIPTION. *External characters.* The width is usually greater than the length, with the greatest width well towards the anterior giving the species a subpentagonal to subtriangular outline.

The beak is strongly developed in the smaller, more triangular specimens but is much less pronounced in the larger ones. Clearly marked beak ridges bound the strongly incurved interarea. An oval, submesothyridid pedicle opening is flanked by strongly conjunct deltoidal plates.

The shell ornament consists solely of very coarse, steep, subangular ribs; the size and coarseness of the ribbing readily distinguishes the species from *S. arduennensis*.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2·58 cm	1·85 cm	2·90 cm
2·40 cm	1·87 cm	2·54 cm

Internal characters. *Pedicle valve.* The dental lamellae are subparallel and relatively short, breaking away from the valve wall well before the insertion of the teeth, as seen in transverse section. The teeth are strong and there are well developed lateral denticulae.

Brachial valve. A septalium is present and consists of strong septalial plates and a relatively weak median septum. The sockets show only weak crenulations; inner and outer socket ridges are well developed.

The crura, which have clearly differentiated bases, are radulifer and curve towards the pedicle valve. At their distal ends they develop the curious processes which are also found in *S. arduennensis*.

DISTRIBUTION. As far as is known, the species has only been recorded from the type locality and from Filey Brigg (E. F. Owen, personal communication 1966).

REMARKS. The species only appears to have been mentioned twice in the literature. In 1878 Davidson tentatively referred the specimen he figured from Wykham to *Rhynchonella lacunosa* Schlotheim and in 1917, Rollier suggested that Davidson's specimen might be *R. helvetica* (Schloth.). As the species does not belong to the “lacunosa group” and *R. helvetica* is here regarded as a nomen dubium, a new species name has been proposed for these forms from the Lower Calcareous Grit.

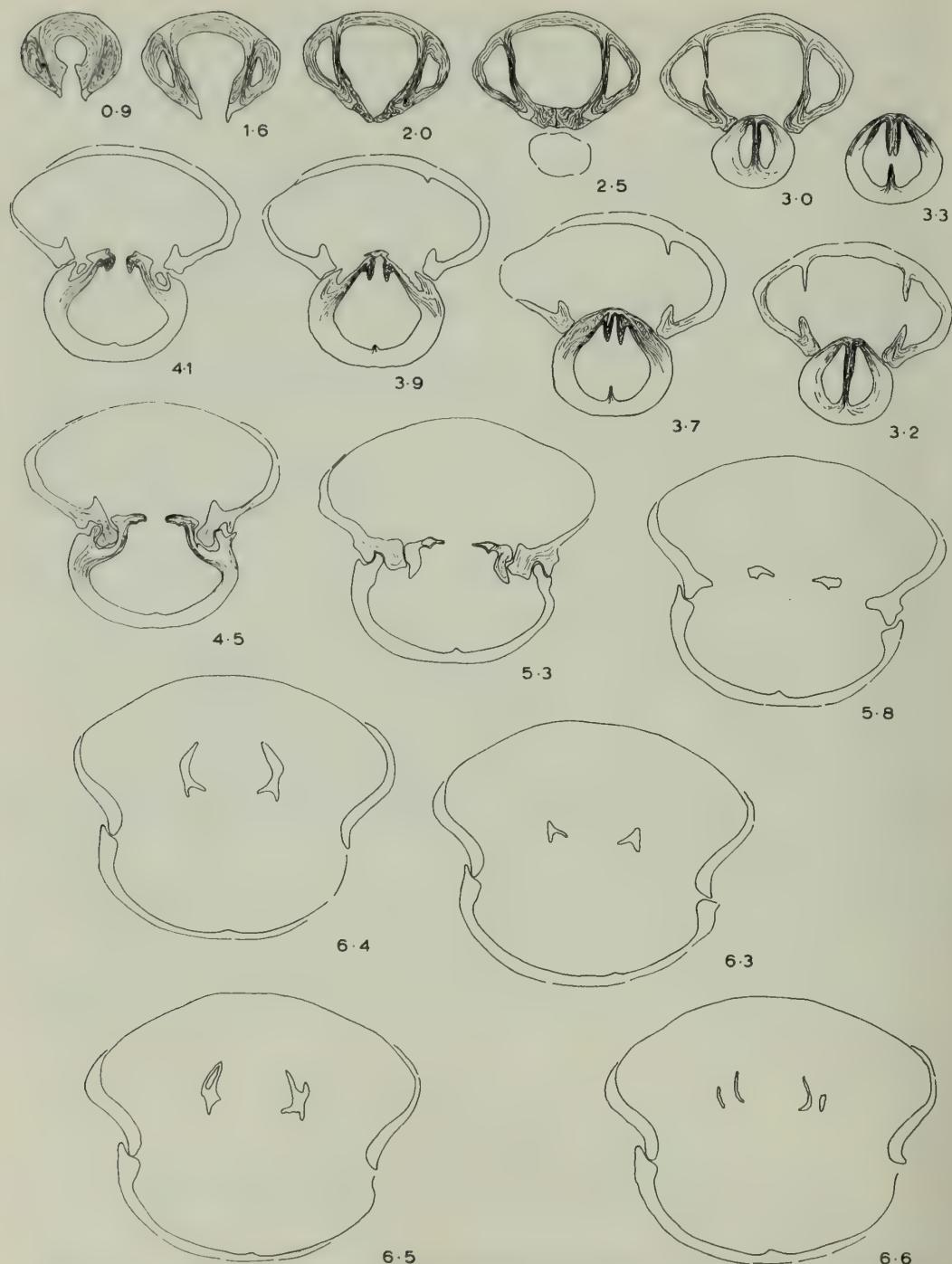


FIG. 33. Transverse serial sections of *Septaliphoria paucicosta* sp. nov. Topotype. Oxfordian. Lower Calcareous Grit. Hutton Bushell, Yorks. B.M. B 26924. ($\times 3$).

***Septaliphoria* (?) *hudlestoni* (Rollier)**
 (Pl. 9, figs. 1-4)

- 1878 *Rhynchonella pinguis* Roemer; Davidson: 193-94, pl. 16, fig. 7.
 1878 *Rhynchonella pinguis* var. *pectunculoides* Etallon; Davidson: 194-95, pl. 16, figs. 8-12.
 1917 *Rhynchonella Hudlestoni* Rollier: 172.
 1933 *Rhynchonella corallina* Leymerie; Arkell: 435.
 1947 *Rhynchonella pinguis* Roemer; Arkell: 87.

EMENDED DIAGNOSIS. Medium to large *Septaliphoria*-like form ; 15-20 coarse, subangular ribs ; uniplication in anterior commissure symmetrically or asymmetrically developed.

STRATIGRAPHICAL RANGE. Kimmeridgian—*cymodoce* zone.

TYPE SPECIMEN. Lectotype, here selected, fig. 10, plate 26 in Davidson (1878) ; collected from Abbotsbury Ironstone, Dorset. B.M. B. 27333.

MATERIAL. 34 specimens in the collection of the B.M.(N.H.) from Abbotsbury, Dorset, B. 26853-54, B. 26856, B. 26858, B. 26859. 8 specimens in author's collection, (from the same locality).

DESCRIPTION. *External characters.* In general the specimens are very poorly preserved. The species appears to be very variable ; many of the specimens show asymmetrical development of the uniplication in the anterior commissure, although never the "bilobed" type of asymmetry found in *Torquirhynchia*. The globose specimens tend to show asymmetry more than the flatter ones which are often weakly trilobate in appearance ; the latter forms also have a higher and more pronounced beak.

The beak ridges are very weak and the interarea is narrow and incurved. It would appear that the pedicle opening is small and circular but details of both this and the deltidial plates have not been satisfactorily observed. Radial ornament consists of about 15-20 coarse subangular ribs, while the only concentric ornament observed has been a few very weak growth lamellae on exceptionally well preserved specimens.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·00 cm	2·60 cm	3·24 cm
2·73 cm	1·98 cm	2·78 cm
2·54 cm	1·70 cm	3·10 cm

Internal characters. An attempt was made to section an apparently well preserved specimen. Unfortunately, the external appearance was deceptive and virtually nothing could be seen of the internal structures except that a median septum and a possible septalium were present in the brachial valve. Mr. E. F. Owen (personal communication 1966) stated that he has attempted to section several specimens and in all cases it was impossible to determine the internal structure.

DISTRIBUTION. The only known occurrence of the species is in the Abbotsbury Ironstone of Dorset.

OCCURRENCE. According to Arkell (1933), the brachiopods are restricted to the "ore bed" which he described as attaining a maximum thickness of 20 feet and as being a "crumbling reddish-brown oolitic rock, full of shining pellets of ore". The rhynchonellids are among the least abundant elements of a fauna which also includes the terebratulid *Ornithella lampas* (Sowerby), and various gasteropods, lamellibranchs and ammonites.

REMARKS. It has been decided to retain the specific name given by Rollier (1917) in preference to *Rhynchonella pinguis* Roemer and *R. pinguis* var. *pectunculoides* Etallon suggested by Davidson in view of the uncertainty attached to those names. If and when the latter species is revised, it may prove necessary to place the name *hudlestoni* in synonymy. This is considered unlikely, however, as the figures of *pectunculoides* given by Etallon (1861) appear to have finer ribs and a much stronger, more upright beak. *Rhynchonella corallina* Leymerie, the specific name suggested by Arkell, seems to be generally accepted as a synonym of *R. pinguis* Roemer, a species frequently quoted but greatly in need of elucidation and revision.

Septaliphoria (?) *septentrionalis* sp. n.
(Pl. 8, figs. 6-7)

NAME. Latin, *septentrionalis*—northerly; the species is only known to occur in the north of Scotland.

DIAGNOSIS. Flattened, medium sized *Septaliphoria*-like form; 10-15 strong, simple ribs; width greater than length.

STRATIGRAPHICAL RANGE. ? Upper Oxfordian—? Lower Kimmeridgian.

TYPE SPECIMEN. Holotype, BB. 44175, collected from Alt-na-cuile, near Brora, Sutherland.

DIMENSIONS OF HOLOTYPE. Length 2.37 cm, thickness 1.45 cm, width 2.86 cm.

MATERIAL. Further 20 specimens collected by the author from Alt-na-cuile; 6 specimens from collection of Royal School of Mines, presumably from the same locality. All the specimens are preserved as sandstone casts.

DESCRIPTION. *External characters.* The shell is either equally biconvex or with a slightly more inflated brachial valve. The beak is quite strong and suberect; details of the beak ridges and interarea are not preserved.

The only ornament preserved is the strong, simple ribs. Some specimens possess a posterior smooth area but it is not certain whether or not this is a result of the poor preservation. A slight uniplication was probably developed in some specimens, but in the best preserved material the anterior commissure tends to be asymmetrical.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2.40 cm	1.73 cm	2.75 cm
2.35 cm	1.42 cm	2.85 cm

Internal characters. The preservation precludes serial sectioning and only very limited information can be obtained from the casts.

The dental lamellae are strong and divergent. The median septum also appears to be well developed and a possible septalium is indicated by one specimen.

DISTRIBUTION. The species is only known from the type locality.

OCCURRENCE. The species is found in the Alt na Cuile Sandstone which Arkell (1933) described as consisting of "thick beds of white sandstone separated by black carbonaceous layers". The associated fauna consists of lamellibranchs and ammonites ; the rhynchonellids are the most abundant element of the fauna.

REMARKS. According to Arkell, the Alt na Cuile Sandstone has not yet yielded ammonites capable of defining precisely the zones present, although it is undoubtedly either topmost Oxfordian or basal Kimmeridgian. As the main fossil band is towards the top of the unit, it seems probable that the rhynchonellids are basal Kimmeridgian in age.

Arkell suggested that, as the rhynchonellids were the best preserved element of the fauna, it might be possible to use them to give a more accurate date to the strata. Unfortunately, there do not seem to be comparable forms of this age on the continent, probably as that area was largely occupied by coral and sponge reef facies, with their specialized faunas, while the Alt na Cuile Sandstone almost certainly represents a limited near-shore facies with a fauna presumably adapted to those conditions.

Although the poor preservation makes generic identification rather hazardous, the species is tentatively referred to *Septaliphoria* Leidhold. This determination is based on the relatively coarse, simple ribs and the fact that the anterior commissure may show either a symmetrical uniplication or be slightly asymmetrical ; the internal characters visible are consistent with this designation ; however, without more detailed information of the internal structures, which is unlikely to be forthcoming, it is not considered that a definite generic diagnosis is possible. Davidson (1878) suggested that the casts from Alt-na-cuile, "may also probably be referable to Schlotheim's species (*Rhynchonella lacunosa*)". It can be safely stated that *S. (?) septentrionalis* does not belong to the genus *Lacunosella*.

Genus *TORQUIRHYNCHIA* nov.

- 1886 *Inconstans-Sippe* (pars) Rothpletz, p. 91.
 1918 *Rhactorhynchia* (pars) Buckman, pp. 50–52.
 1932 *Septaliphoria* (pars) Wiśniewska, pp. 18–20.

NAME. Latin *se torquere*—to twist : all members of the genus are markedly asymmetrical.

TYPE SPECIES. *Terebratula inconstans* Sowerby.

DIAGNOSIS. Large, asymmetrical rhynchonellids with coarse, simple ribbing ; septal plates reduced or absent ; median septum present but usually very weakly developed ; crura radulifer.

STRATIGRAPHICAL RANGE. In Europe the species appears to be restricted to the Kimmeridgian and lower Volgian ; however, Makridin (1964) has figured specimens from the Russian Platform which appear to belong to *Torquirhynchia* and which include material from the upper Oxfordian and the middle and upper Volgian.

DESCRIPTION. *External characters.* The most characteristic feature is the strong asymmetry exhibited by all the species, as viewed from the anterior. The "twist" occurs indiscriminately either to the right or to the left. A fold and uniplication are never developed. Each valve has 20–30 angular or subangular ribs which are almost invariably simple, arising from the umbones; however, bifurcation has occasionally been observed postero-laterally in *T. guebhardi* and *T. speciosa*.

The strong beak is usually suberect although in specimens with a very inflated brachial valve, notably in *T. inconstans*, it may be adpressed to that valve. Except in the latter case, a functional pedicle opening is present and is flanked by disjunct to strongly conjunct deltoidal plates.

Internal characters. Pedicle valve. The lateral cavities and dental lamellae are rather variably developed, ranging between massive lamellae and correspondingly small lateral cavities and larger cavities bounded by slender lamellae. A slight pedicle collar may be developed. Strong, crenulated teeth and well developed lateral denticulae characterize the hinge apparatus.

Brachial valve. A low, relatively long median septum is present; septalial plates occur in all the species investigated, although they are of a distinctively reduced form. Inner and outer socket ridges are both well developed; the socket floors are strongly crenulated.

The crural bases differ quite markedly in their development in the different species described. Although the crura are radulifer in general appearance, they show considerable variation towards their distal ends. It is not known whether the development of these various distal processes can be regarded as consistent at species level.

SPECIES. The following nominal species are attributed to the genus:

- T. "astieriana"* (Orbigny) (in Haas, 1891, p. 62, pl. viii, figs. 3–6, pl. ix, figs. 1–9)
- T. "astieriana"* (Orbigny) (in Makridin, 1964, pp. 107–9, pl. ii, fig. 8)
- T. "astieriana"* (Orbigny) (in Wiśniewska, 1932, p. 20, pl. i, figs. 21–26)
- T. astieriiformis* (Wiśniewska) (1932, pp. 27–28, pl. i, figs. 19 ?20)
- T. inconstans* (Sowerby) (1821, vol. III, p. 137, pl. 277, fig. 4)
- T. guebhardi* (Jacob & Fallot) (1913, p. 44, pl. v, fig. 9)
- T. pseudo-inconstans* (Kitchin) (1900, pp. 51–2, pl. x, figs. 6–10)
- T. lemanni* (Makridin) (1964, pp. 109–10, pl. ii, fig. 9)
- T. pectunculoides* (Etallon) (1861, p. 289, pl. xlvi, fig. 3)
- T. semiconstans* (Etallon) (1861, p. 290, pl. xlvi, fig. 4)
- T. speciosa* (Münster) (1839, p. 113, pl. xiii, fig. 6).

DISTRIBUTION. Although individual species appear to be relatively restricted geographically, the genus, taken as a whole, occurred over much of Europe west of the Alps. If the species of Makridin mentioned above have been correctly assigned, then the genus was also present on the Russian Platform.

OCCURRENCE. The genus appears, from the limited information available, to have been restricted to peri-reef areas, and it is suggested that the asymmetrical development may represent an adaptation for living in a high energy environment.

REMARKS. The genus *Torquirhynchia* has been proposed in order to group together the various distinctively asymmetrical rhynchonellid species of the Upper Jurassic. Many of the included species have previously been attributed to *Rhynchonella astieriana* Orbigny.

The Upper Jurassic, asymmetrical rhynchonellids have also been frequently referred to the genus *Septaliphoria* Leidhold, largely as a result of the paucity of generic names at this stratigraphical level and the lack of information regarding the diagnostic characters of the type species of that genus, namely *S. arduennensis* (Oppel). Internally, *Torquirhynchia* is readily distinguished from *Septaliphoria* by its weakly developed septalial plates and the position and development of the crural bases relative to them. Externally, the adult specimens of *Torquirhynchia* attain a much greater size and are always strongly asymmetrical whereas specimens of *Septaliphoria* are only weakly asymmetrical or are symmetrical.

***Torquirhynchia inconstans* (J. Sowerby)**

(Pl. 10, figs. 1-3, pl. 12, fig. 5, text-fig. 34)

- 1821 *Terebratula inconstans* J. Sowerby: 137, pl. 278, fig. 4.
- 1834 *Terebratula inconstans* J. Sowerby; Buch: 45-46.
- 1838 *Terebratula inconstans* J. Sowerby; Buch: 146, pl. 14, fig. 16.
- 1852 *Rhynchonella inconstans* (J. Sowerby); Davidson: 87-88, pl. 18, figs. 1-3.
- 1878 *Rhynchonella inconstans* (J. Sowerby); Davidson: 191-93, pl. 16, figs. 1-6.
- 1917 *Rhynchonella inconstans* (J. de C. Sowerby) (sic); Rollier: 177-78.
- 1918 *Rhactorhynchia inconstans* (J. Sowerby); Buckman: 51.

EMENDED DIAGNOSIS. Medium sized, globose *Torquirhynchia*; strongly developed beak ridges and interarea; 25-30 simple angular ribs; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—*baylei* to *cymodoce* zones.

TYPE SPECIMEN. Lectotype, here selected, fig. 4, pl. 277 of Sowerby (1821); the specimen is from the Kimmeridge Clay of Ringstead Bay, Dorset, in B.M.(N.H.) Sowerby Coll. No. B. 61475.

MATERIAL. More than 100 specimens from the collection of the B.M.(N.H.) mostly from the Dorset Coast but also including a limited number of specimens from inland localities. 10 specimens in the author's collection obtained from Ringstead Bay.

DESCRIPTION. *External characters.* The shell outline is subpentagonal and the valves are equally biconvex. The radial ornament consists of about 25-30 simple, angular or subangular ribs which show neither intercalation nor bifurcation, while the concentric ornament consists of numerous fine growth lines and occasional weak growth lamellae. In the flatter specimens the strongly developed beak is erect but the extent of the incurvature is obviously dependent on the globosity of the shell and in very globose specimens the beak is adpressed to the brachial valve.

The relatively small hypothyridid or submesothyridid pedicle opening is flanked by small disjunct or conjunct deltoidal plates. Beak ridges are clearly marked and bound the well developed interarea; the latter may be flattened but is usually strongly incurved.

The asymmetrical development usually commences when the animal is about half grown and becomes increasingly pronounced with age.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·20 cm	3·10 cm	3·25 cm
3·02 cm	2·64 cm	3·12 cm
3·20 cm	2·25 cm	3·31 cm

Internal characters. *Pedicle valve.* The shell wall is very thick and the small lateral cavities are not seen in transverse section until about the level of the top of the brachial valve. The dental lamellae are massive and only attached to the ventral shell wall at their extreme posterior ends. The teeth are strong and heavily crenulated ; the general impression given by the teeth, dental lamellae and the way the pedicle valve abuts against the brachial valve in the earlier sections, is that the species possessed a very strongly articulated shell.

Brachial valve. The sockets are crenulated and there are both inner and outer socket ridges. A median septum is present but it does not come into contact with the septal plates as it is only present posteriorly as a low ridge. The septum completely disappears, as seen in transverse section, before the end of the crura is reached, but shows quite a strong development for part of its length. The distinctive short, rounded septal plates are seen on the dorsal side of the ventrally curved hinge plates. Crural bases are hardly differentiated. At first, as seen in transverse section, the radular crura appear as structures flattened in the plane of articulation, but in later sections they become more rod-like and finally become flattened at right angles to the plane of articulation and curve towards the pedicle valve.

DISTRIBUTION. The best known localities are those of Ringstead Bay and Weymouth in Dorset ; inland, it has been recorded from Shotover Hill near Oxford, Wooton Bassett in Wiltshire, Brill in Buckinghamshire and from Swindon. On the continent as observed by Haas (1890), the species appears to be restricted to north-western France. Buch (1838) recorded it from Ellrichserbring in Brunswick. His figure of the species is a copy of Sowerby's (1821) figure 4 and, as he did not illustrate any material from his locality, the record must be regarded as doubtful.

OCCURRENCE. At Ringstead Bay it occurs in a thin bed of pale grey clay, lying between the Ringstead Coral Bed and the Exogyra Bed, as illustrated in Arkell (1933, pl. 21). The associated fauna includes terebratulids, the gasteropod *Bathrotomaria reticulata* (Sowerby) and ammonites. Ager (1965a) has drawn attention to the probability of *T. inconstans* living in a peri-reefal environment, as evidenced by the close proximity of the Coral Bed. At Shotover Hill it is recorded by Phillips (1855) as occurring in a band of septarian nodules in a shaly clay of *cymodoce* age.

REMARKS. In his discussion of the species, Davidson (1852) included a specimen (pl. 18, fig. 4) from the Inferior Oolite of Leckhampton Hill. The author has not seen the actual specimen, but assumes this to be a misidentification in view of the otherwise restricted record of the species. On the same plate fig. 3, Davidson figured a symmetrical specimen from Shotover Hill, again the author has not seen the

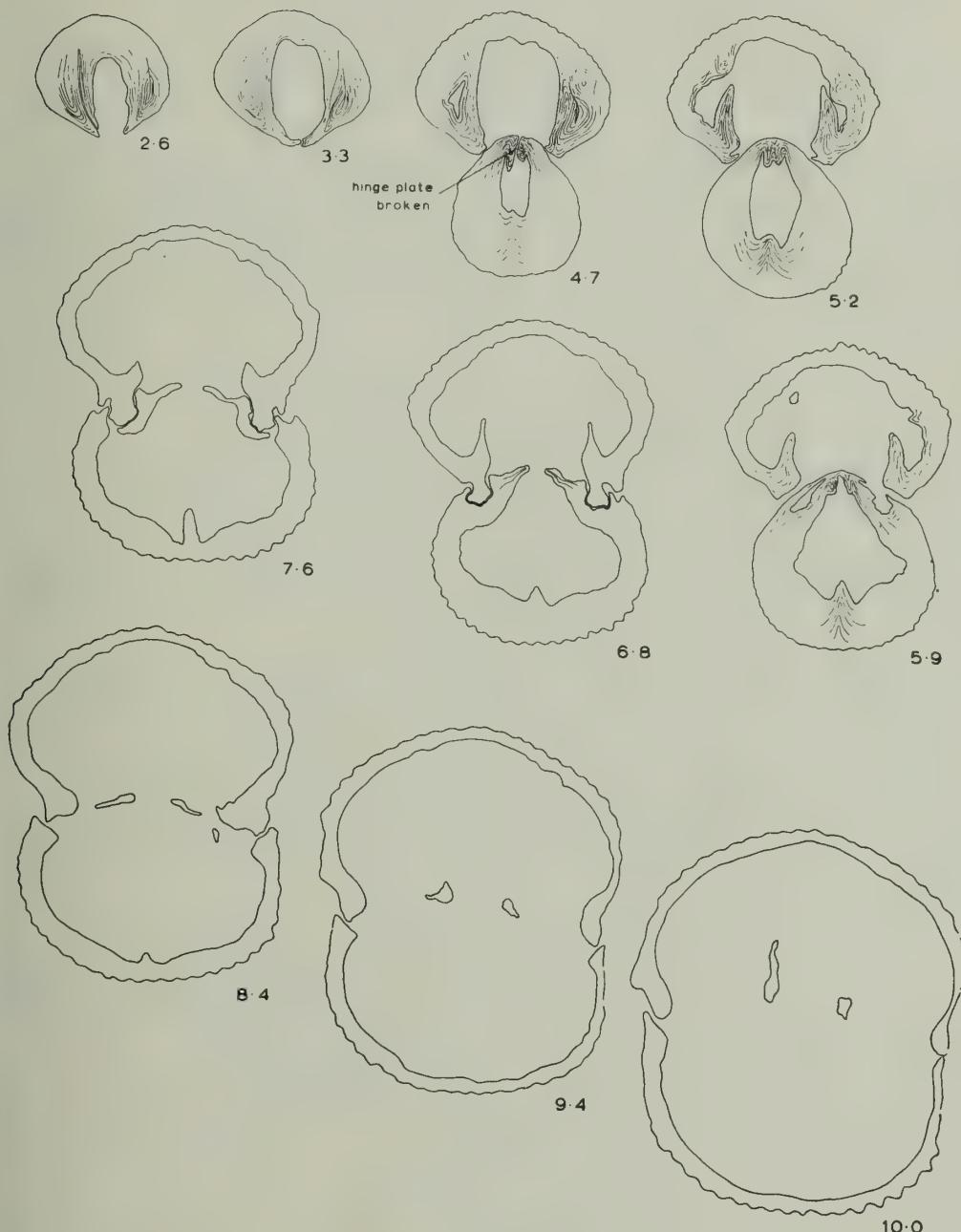


FIG. 34. Transverse serial sections of *Torquirhynchia inconstans* (Sowerby). Topotype. Kimmeridgian. Kimmeridge Clay. Ringstead Bay, Dorset. ($\times 2$).

specimen but it seems unlikely that it is correctly determined as, apart from its symmetry, the ribbing and general shape also differ from *inconstans*. The B.M. (N.H.) collection contains only one symmetrical specimen attributed to *inconstans*, a large trilobate form again from Shotover Hill. The horizon of this specimen is not known but, despite crushing, it is interesting in that it appears closer to *Somalirhynchia sutherlandi* than to *T. inconstans*.

While collecting material at Ringstead Bay, it was obvious that a fairly high proportion of the specimens obtained were unusual in that the valves "gaped". The author has since examined the specimens available at the B.M.(N.H.), about 100, and this has confirmed that about a third show this feature. Many specimens have a well developed epifauna and the tubes of *?Serpula* are frequently seen on both valves.

***Torquirhynchia guebhardi* (Jacob & Fallot)**

(Pl. 10, figs. 4-6, text-fig. 35)

- 1913 *Rhynchonella Astieriana* Orbigny var. *Guebhardi* Jacob & Fallot: 45-46, pl. 5, fig. 9.
 1917 *Rhynchonella Guebhardi* Rollier: 77.

EMENDED DIAGNOSIS. Medium-sized, globose *Torquirhynchia*; markedly asymmetrical with a frontal notch between the two lobes; about 30 subangular ribs; radulifer crura flattened in the plane of articulation.

STRATIGRAPHICAL RANGE. Jacob & Fallot describe it as coming from the "Portlandien"; the author has collected it from the *cymodoce* zone of the Kimmeridgian.

TYPE SPECIMEN. Lectotype, here selected, the specimen figured by Jacob & Fallot (1913), pl. 5, fig. 9; the type locality is St. Vallier (Alpes-Maritimes).

MATERIAL. 7 specimens from a road cutting north of Lac d'Armaille (Ain) in British Museum (Nat. Hist.) nos. BB. 45762-68. Other localities in the southern Jura from which the species has been collected include Rossillon, Glandieu, Brognin Hill and Chavoley.

DESCRIPTION. *External characters.* The valves are almost equally biconvex, with a tendency for the brachial to be slightly the more inflated. However, the valves are distinctively very globose and this, coupled with the very strongly developed asymmetry, differentiates *T. guebhardi* from other species in the genus. The beak is sharp and suberect and the shell outline subtriangular.

T. guebhardi possesses about 30 relatively fine, subangular ribs which arise at the umbones and continue simply to the anterior margin; bifurcation has only been observed in a few postero-laterally positioned ribs. The concentric ornament consists only of rather sparse, weak growth lamellae.

Although the beak is quite large and suberect, the beak ridges are only weakly developed as are the small, incurved interareas. An oval, submesothyridid pedicle opening is flanked by conjunct deltidial plates. In transverse section the deltidial plates are clearly seen to project externally around the foramen.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
2·97 cm	2·20 cm	3·35 cm
2·55 cm	1·95 cm	2·80 cm

Internal characters. Most of the fine detail of the structures has been lost through recrystallisation.

Pedicle valve. The narrow, elongate lateral cavities, which penetrate almost to the apex of the beak, are limited by slender dental lamellae. A pedicle collar is present. The teeth are strong and crenulated; lateral denticulae are present but not strongly developed.

Brachial valve. There is no septalium and only a weak median septum; small septalial plates are present. The sockets are crenulated; inner and outer socket ridges well developed. Crural bases are not well differentiated. The radulifer crura are flattened in the plane of articulation and do not curve towards the pedicle valve.

DISTRIBUTION. The species only appears to have been recorded from the following two areas. (1) The material of Jacob & Fallot (1913) came from St. Vallier in the French Alpes Maritimes and in the "Portlandien coralligène des environs de Gerin, Ain". The latter name is probably a mis-spelling of Cerin. (2) All the material studied by the author was collected by various members of Imperial College from the southern French Jura in the area around Belley, which is also in the Département of Ain.

OCCURRENCE. The material described by the author was collected from the Bedded Virieu Limestone (Ager and Evamy, 1963). The following description of mode of occurrence and lithology is taken from Evamy (1963), "The subdivision (of the Bedded Virieu containing *T. guebhardi*) is about 20 m thick—it consists mainly of alternating limestones and shales, which yield an abundant brachiopod, lamellibranch fauna, as well as ammonites of the *tenuilobatum* and *pseudomutabilis* zones—. The limestones are thinly bedded (20–40 cm) brown calcilutites, occasionally showing a mottled iron-staining. These are separated by thin (approximately 10 cm) shaly bands." He also noted that, "A few thicker beds of calcilutite (1–1½ m) are seen not to contain the abundant mollusc and brachiopod fauna." The beds containing *T. guebhardi* immediately underlie the reef horizon of the Massive Virieu Limestone.

REMARKS. Although the author has not seen the original material of *Rhynchonella Astieriana* var. *Guebhardi*, it is thought that a conspecific identification for the material from the Bedded Virieu Limestone can confidently be given as it matches exactly the specimen figured by Jacob & Fallot (1913). Also, the Bedded Virieu could well be the lateral stratigraphical equivalent of the "Portlandien" of Jacob and Fallot. Referring to the Bedded Virieu, Ager and Evamy (1963) note that it is, "strongly reminiscent of the 'Tithonian' facies seen in many parts of Europe at this level". In the latter publication, *T. guebhardi* is referred to as *Septaliphoria astieriana* (d'Orbigny).

JURASSIC RHYNCHONELLIDS

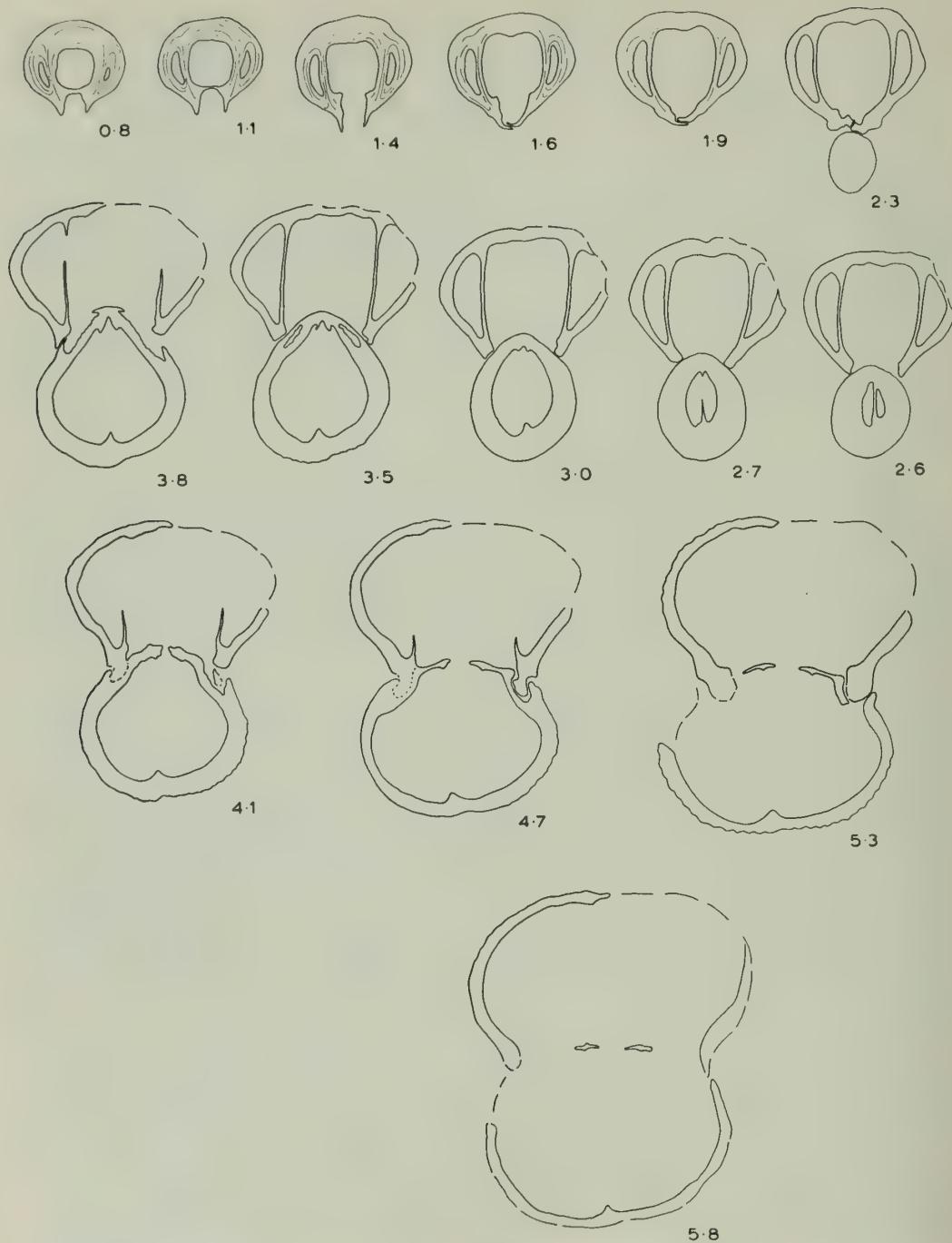


FIG. 35. Transverse serial sections of *Torquirhynchia guebhardi* (Jacob & Fallot). Kimmeridgian—*cymodoce* zone. N. of Lac d'Armaile (Ain), France. ($\times 3$).

Torquirhynchia cf. *T. astieriformis* (Wiśniewska)
 (Pl. 12, figs. 1–3, text-fig. 36)

1932 *Septaliphoria pinguis* (Roemer) var. *astieriformis* Wiśniewska: 27–28, pl. 1, fig. 19, ?20.

EMENDED DIAGNOSIS. Relatively flattened, medium sized *Torquirhynchia*; about 20 subangular ribs; beak small; asymmetrical development not sufficient to produce a frontal notch; crura radulifer.

STRATIGRAPHICAL RANGE. The material described by the author came from the *mutabilis* zone of the Kimmeridgian, while the specimens figured by Wiśniewska came from the “Rauracien sup.” and “Kimmeridgien?”

MATERIAL. 6 specimens collected by the author from Sermérieu (Isère), including B.M. BB.45174, BB.45175, BB.45176.

DESCRIPTION. *External characters.* The width is greater than the length and the greatest width is towards the anterior; this, combined with the rather steep apical angle, results in an overall subtriangular outline. *T. cf. T. astieriformis* is equally biconvex and relatively flattened as compared with other species of the genus. The coarse ribs arise at the umbones and continue simply to the anterior margin; concentric ornament has not been observed.

The beak is suberect and flanked by slight beak ridges which delimit the weakly developed and slightly incurved interarea. Disjunct deltidial plates define the relatively small pedicle opening. Asymmetry is characteristic but is not so marked as in *T. guebhardi* as it does not result in the development of a frontal notch.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
3·18 cm	2·55 cm	3·49 cm
2·63 cm	2·94 cm	3·00 cm
2·32 cm	2·47 cm	2·73 cm

Internal characters. Pedicle valve. The lateral cavities are bounded by strong, subparallel dental lamellae which break away from the ventral wall of the valve, as seen in transverse section, before the insertion of the teeth. The teeth are strong and crenulated; well developed lateral denticulae are present.

Brachial valve. The sockets show tegulate crenulations and both inner and outer socket ridges are strongly developed. The radulifer crura curve towards the pedicle valve; at their distal ends they produce the rather peculiar processes seen in text-fig. 36.

DISTRIBUTION. As stated above, the author's material came from Isère where, according to Dr. Enay (personal communication 1964), it is not an uncommon species. The only figured material likely to be conspecific is that of Wiśniewska (1932) from Poland.

OCCURRENCE. The species was collected from irregularly interbedded, fine grained limestones and marls. The exposure consisted of a small roadside cutting and the varied fauna present was largely collected from around a small sponge reef about 1 m high and 2 m across. Apart from the rhynchonellids, the fauna included

JURASSIC RHYNCHONELLIDS

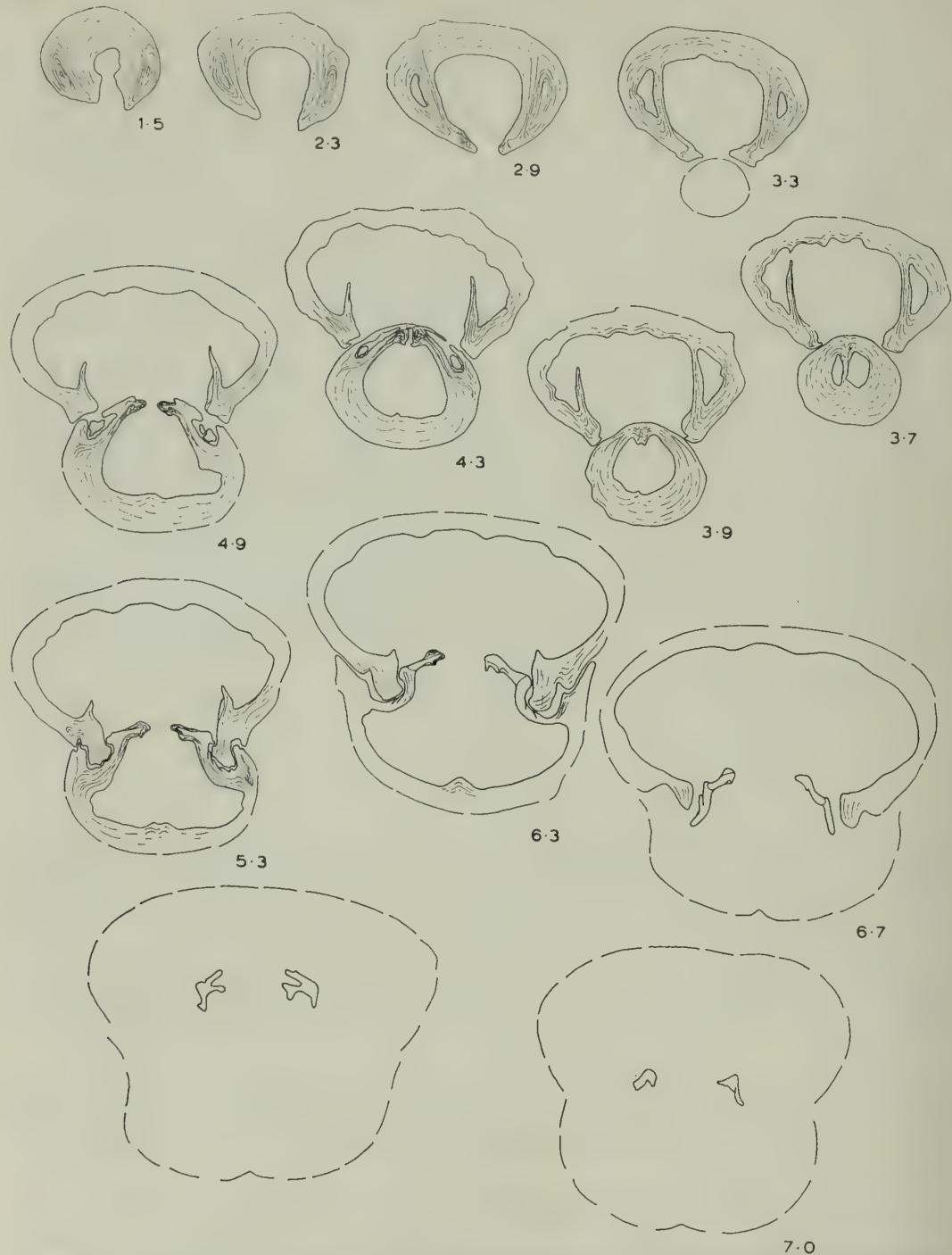


FIG. 36. Transverse serial sections of *Torquirhynchia* cf. — *astieriformis* (Wiśniewska). Kimmeridgian—*mutabilis* zone. Sermétrieu (Isère), France. ($\times 3$).

crinoid ossicles, zeilleriids and terebratulids as well as sponges. The rhynchonellids were interesting in that the two species present belonged to two different genera namely, *Torquirhynchia* and *Lacunosella*; both species were associated with the sponges and Dr. Enay stated that this is a characteristic association of the *mutabilis* zone in that area. *T. cf. astieriformis* was the least abundant element of the fauna.

REMARKS. Although externally one, at least, of the specimens figured by Wiśniewska very closely resembles the material from Isère, the lack of records from the intervening area and the lack of knowledge as to the internal structures of the Polish material precludes a definite conspecific identification of the French and Polish specimens.

***Torquirhynchia speciosa* (Münster)**
(Pl. 11, figs. 1-3, text-fig. 37)

- 1832 *Terebratula difformis* Lamarck; Zieten: 56, pl. 62, figs. 2.
- 1839 *Terebratula inconstans speciosa* Münster: 113, pl. 13, fig. 6.
- 1847 *Rhynchonella Astieriana* Orbigny: 14-15, pl. 492, figs. 1-4.
- 1850 *Rhynchonella Astieriana* Orbigny: 24.
- 1852 *Terebratula inconstans* Quenstedt: 455, pl. 36, fig. 44.
- 1858 *Rhynchonella Astieriana* Orbigny; Suess: 52, pl. 6, fig. 2.
- 1863 *Rhynchonella inconstans* Orbigny; Ooster: 47, pl. 15, figs. 1-13.
- 1871 *Terebratula inconstans speciosa* Quenstedt: 138-39, pl. 15, figs. 45, 51, ?50.
- 1885 *Terebratula inconstans* Quenstedt: 694, pl. 53, fig. 64.
- 1913 *Rhynchonella Astieriana* Orbigny; Jacob & Fallot: 43, pl. 5,
- 1917 *Rhynchonella Astieriana* Orbigny; Rollier: 176.
- 1917 *Rhynchonella speciosa* Rollier: 178.

EMENDED DIAGNOSIS. Largest known species of *Torquirhynchia*, being up to 10 cm wide; 20-30 coarse, angular ribs; large prominent suberect beak; asymmetrical; width always greater than length; crural bases sharply pointed; crura radulifer.

STRATIGRAPHICAL RANGE. Kimmeridgian—lower Volgian: limestones in which topotypes occur range from *subeumela* to *Gravesia* zones (Dr. Barthel, personal communication 1965).

TYPE SPECIMEN. Lectotype, here selected, is the specimen originally figured by Münster, pl. 13, fig. 6; a plaster cast of this is in the collection of the B.M.(N.H.), B. 5513.

DIMENSIONS OF LECTOTYPE. Taken from plaster cast mentioned above: length 5.22 cm, thickness 3.35 cm, width 7.92 cm.

MATERIAL. 28 specimens in the collection of the author including B.M. BB.45171, BB.45173 from Saal, Germany. 2 specimens from collection of the University of Tübingen.

DESCRIPTION. *External characters.* *T. speciosa* is one of the largest Mesozoic rhynchonellids: Quenstedt (1871) recorded a specimen over 10.0 cm wide. The species shows considerable variation in outline but, as the greatest width is well toward the anterior, it is usually subtriangular or suboval. There are about 20-30

very strong, sharply angular ribs which arise from the umbones and continue simply to the anterior margin. Concentric ornament, not always preserved, consists of numerous fine growth lines, together with occasional coarser growth lamellae.

The species has a characteristically strong, high, suberect beak which is flanked by a large, well-marked interarea, although the beak ridges limiting these are only weakly developed. *T. speciosa* possesses a large hypothyridid pedicle opening.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
5.50 cm	2.30 cm	6.87 cm
4.73 cm	2.42 cm	5.00 cm
2.60 cm	1.70 cm	3.05 cm

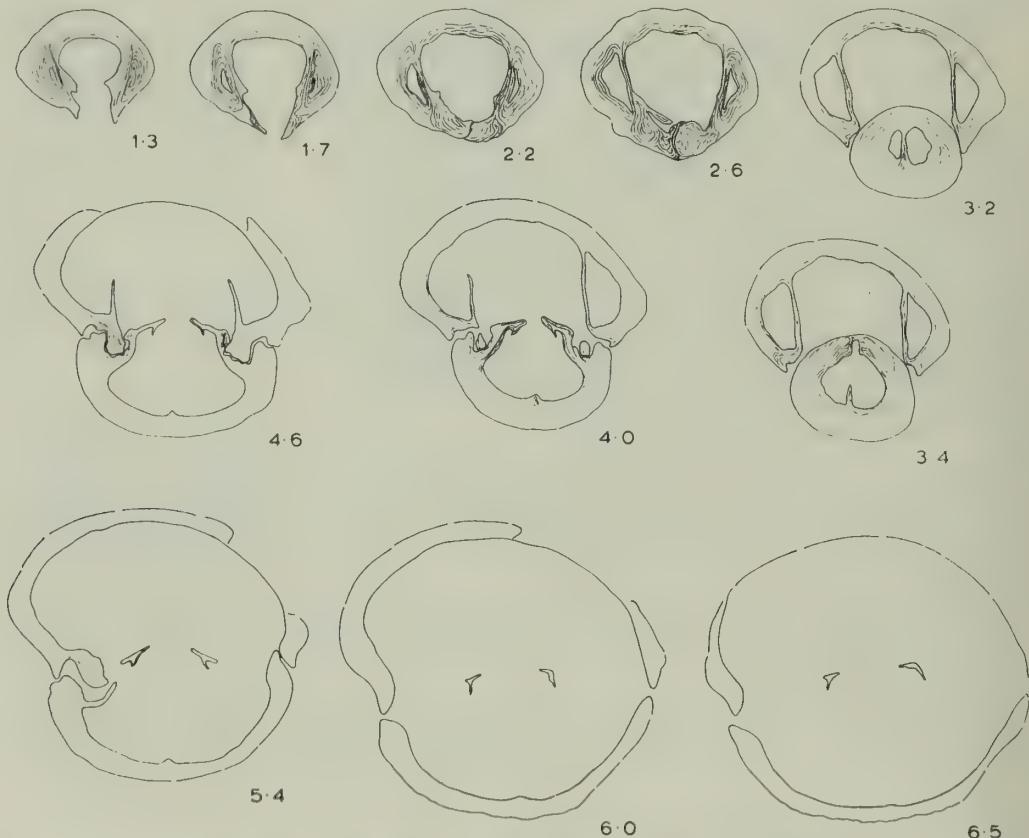


FIG. 37. Transverse serial sections of *Torquirhynchia speciosa* (Münster). Kimmeridgian/Lower Volgian. "Dieras Kalk". Saal, Germany. ($\times 3$).

Internal characters. Pedicle valve. There is a weakly developed pedicle collar. The deltidial plates project slightly, "reinforcing" the pedicle opening; below the level of the pedicle opening they become conjunct and then "crumple up" against one another. Relatively slender, subparallel dental lamellae are present. The teeth are strong and crenulated; there are well developed lateral denticulae.

Brachial valve. The median septum is weak and there are no septalial plates. The crural bases are clearly differentiated. The radulifer crura are relatively small and curve only slightly to the ventral of the plane of articulation. The sockets show tegulate crenulations ; inner and outer socket ridges are both strongly developed.

DISTRIBUTION. Judging from the figures and descriptions in the literature, the species has a rather discontinuous distribution. The material figured by Zieten (1832), Münster (1839) and Quenstedt (1852, 1871, 1885) came from the Franconian and Swabian Jura, while the type localities for *Rhynchonella Astieriana* of Orbigny (1847) are in the French "Alpes Maritimes" at Escragnolles and La Malle. Other figured specimens which would appear to be conspecific are from "Les Alpes Bernoises et Vaudoises" (Ooster, 1863), and from Stramberk, Czechoslovakia, and adjacent areas of Poland (Suess, 1858).

OCCURRENCE. At Saal, *T. speciosa* is associated with a very varied fauna which includes many large species, or at least large specimens, of terebratulids, gasteropods and lamellibranchs. One of the most distinctive elements here is the lamellibranch *Diceras*, which gives its name to the limestone. Dr. Barthel (personal communication 1965) suggests that the Diceras-Kalk, as seen at Saal and Kelheim, represents a fore-reef limestone. Unfortunately, the details at Saal are largely obscured by the recrystallization, tectonics and fissure infillings of younger material.

REMARKS. Although the name *Rhynchonella Astieriana* of Orbigny (1847) has been very widely used and is embedded in the literature, it is an indisputable objective junior synonym of *Terebratula inconstans speciosa* of Münster (1839). In his original description of *R. Astieriana* Orbigny gave Münster's species in his synonymy and as, under the present rules of nomenclature, it is not permitted to arbitrarily replace a specific or subspecific name with another, Münster's name *speciosa* must be given priority. Since Orbigny, it appears that only Quenstedt (1871) has described *Astieriana* as a synonym of *speciosa* while other authors such as Suess (1858) and Haas (1870) have either retained the name *Astieriana* while admitting *speciosa* as a synonym of it, or ignored *speciosa* altogether, e.g., Jacob and Fallot (1913). In general, the name *Astieriana* has tended to be used for all rhynchonellids in the Upper Jurassic showing asymmetry.

Terebratula difformis of Zieten is a junior homonym of *T. difformis* of Lamarck.

"*Rhynchonella*" *ordinaria* sp. n.

(Pl. 9, figs. 7-11, text-figs. 38-39)

NAME. Latin ordinarius-a-um, ordinary ; the species is a very "ordinary looking" rhynchonellid.

DIAGNOSIS. Medium sized rhynchonellid ; strong suberect beak ; 15-20 simple, subangular ribs ; there is a weak median septum ; septalial plates present but only poorly developed ; crura radulifer.

STRATIGRAPHICAL RANGE. Of the two occurrences of the species known one is in the *pseudocordata* zone of the Oxfordian and the other is in the "Sequanien".

TYPE SPECIMEN. Holotype, BB. 45167, was obtained from the *pseudocordata* zone at Mont Dolet near Sermérieu (Isère), France.

DIMENSIONS OF HOLOTYPE. Length 2·50 cm, thickness 1·78 cm, width 2·20 cm.

MATERIAL. 20 specimens collected by the author from the type locality, British Museum (Nat. Hist.) nos. BB. 45710-19, BB. 45770-79; 30 specimens from near Bourges (Cher) collected by M. Delance, (University of Dijon).

DESCRIPTION. *External characters.* The species is an ordinary looking rhynchonellid with the valves either equally biconvex or with the brachial valve slightly the more inflated. Length and width are about equal and either may be the greater; maximum width may be well toward the anterior or roughly median, thus giving a considerable range of overall outline. The young specimens are more flattened and subtriangular.

Most specimens have a high, strong beak which is flanked by strong beak ridges. The interarea is markedly incurved and is developed most strongly at the base of the beak where it impinges on the brachial valve giving a distinctive bend to the hinge line. A large, circular, hypothyridid pedicle opening is present and is limited by conjunct deltidial plates.

The radial ornament consists of rather coarse, steep, simple ribbing, while the concentric ornament comprises numerous very fine growth lines. The anterior commissure either shows a symmetrical low uniplication or varying degrees of asymmetry; the latter feature is never so strongly developed as in *Torquirhynchia*, but shows the same sort of variation as described for *Septaliphoria*.

DIMENSIONS OF FIGURED SPECIMENS.

length	thickness	width
1·26 cm	0·51 cm	1·25 cm
1·82 cm	0·77 cm	1·66 cm
2·40 cm	1·85 cm	2·17 cm
2·28 cm	1·42 cm	2·18 cm
2·50 cm	1·78 cm	2·20 cm

Internal characters. Pedicle valve. The beak is massive and the sub-parallel dental lamellae are quite short resulting in the development of only small lateral cavities. A small pedicle collar is present. The teeth are strong and crenulated and the species also possesses strong inner and outer socket ridges.

Brachial valve. The hinge plates are arched ventrally and the inner hinge plate is distinctive in showing a dorsally directed ridge flanked by small septalial plates. Crural bases are differentiated; the relatively small radulifer crura curve slightly toward the ventral valve.

DISTRIBUTION. Only known from the type locality and from near Bourges (Cher), France.

OCCURRENCE. The specimens from Isère were collected from a band of fine-grained limestone, about 1·25 m thick, in which they occurred as loose groups. The associated fauna consisted of occasional zeilleriids and lamellibranchs, including oysters. M. Delance, of the University of Dijon, describes his material as coming from a " calcaire crayeux blanc, très friable ", which lies above a massive reef limestone containing corals.

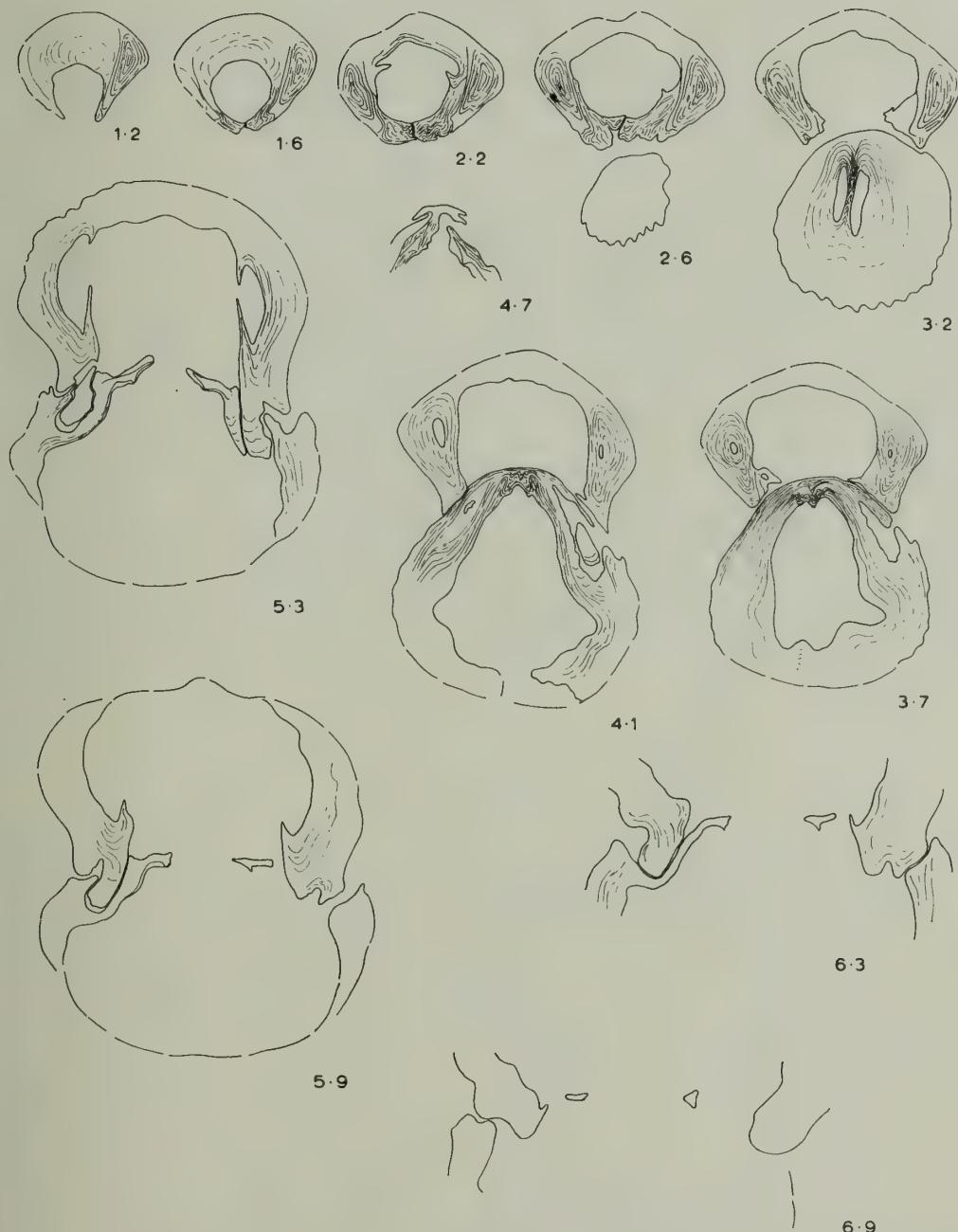


FIG. 38. Transverse serial sections of "*Rhynchonella*" *ordinaria* sp. nov. Topotype. Oxfordian—*pseudocordata* zone. Mont Dolet (Isère), France. ($\times 3$).

JURASSIC RHYNCHONELLIDS

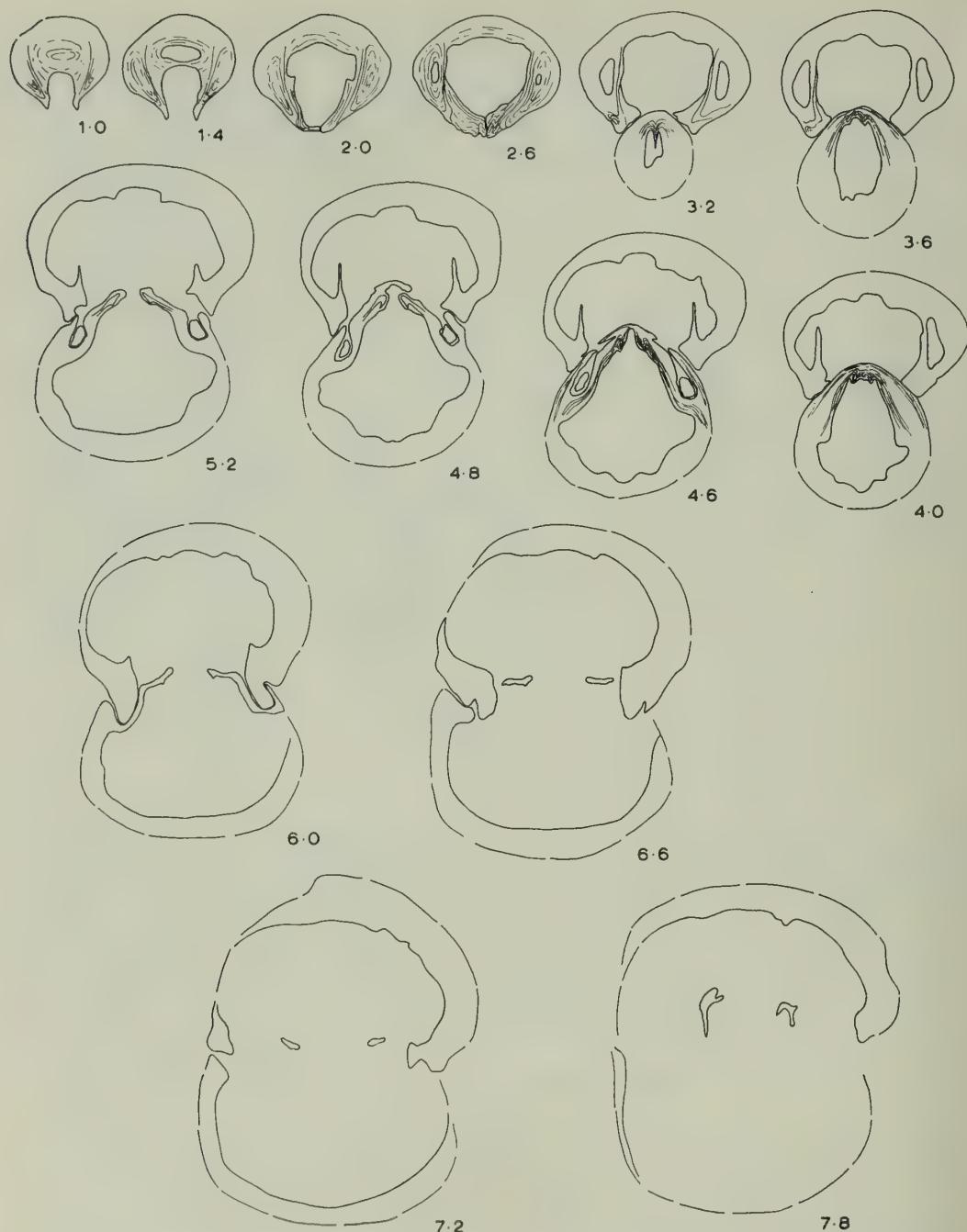


FIG. 39. Transverse serial sections of "*Rhynchonella*" *ordinaria* sp. nov. "Sequanien". Bourges (Cher), France. ($\times 4$).

REMARKS. Externally, the species appears similar to forms such as "*R. hopkinsi*" of the Bathonian which are normally referred to *Burmirhynchia* Buckman. However, there is considerable doubt as to many of the features of that genus and nobody appears to have published serial sections of topotypic material. Mr. E. F. Owen has kindly allowed the author to see sections of a Burmese specimen in the reference collection of the B.M.(N.H.), and while those seem to be closely comparable with those made of "*R.*" *ordinaria*, this in itself is somewhat odd in view of the original description of the genus in which Buckman stressed the prominent nature of the median septum and dental lamellae, features only poorly developed in "*R.*" *ordinaria*. These latter features can be clearly seen in the burnt specimens figured by Buckman (1918) and are also in a specimen attributed to *R. hopkinsi* from Chatillon-sur-Seine, which was sectioned for comparison. Although it is very difficult to judge to what extent such features observed externally will be developed as seen in transverse section, it is considered that their very weak development in "*R.*" *ordinaria* represents a marked discrepancy as compared with the species figured as *Burmirhynchia* by Buckman.

In general shape and form of ribbing, "*R.*" *ordinaria* is also comparable with certain species of the genus *Kallirhynchia* Buckman. Internally, it shows some resemblance to *Kallirhynchia yaxleyensis*, as figured by Muir-Wood (1934), especially in the development of its septalial plates and in the shape of the crura. However, *Kallirhynchia*, as it is at present defined, is restricted to the Bathonian and consequently it seems unwise to place *ordinaria* in that genus until intermediate forms have been described. At present the rhynchonellid faunas of the Bathonian and Callovian are very imperfectly known.

"*Rhynchonella*" *pyrenaei* sp. n.

(Pl. 3, fig. 7, text-fig. 40)

NAME. Latin—Pyrenaeum-i, the Pyrenees ; the type locality is near Pau (Basses-Pyrénées).

DIAGNOSIS. Small to medium sized rhynchonellid ; length greater than width ; beak relatively large and suberect ; about twelve ribs, some of which bifurcate ; low uniplication ; crura radulifer.

STRATIGRAPHICAL RANGE. Lower Oxfordian.

TYPE SPECIMEN. Holotype from the Pic du Gar near Pau (Basses-Pyrénées). BB. 45161.

MATERIAL. Large number of broken and poorly preserved specimens in the author's collection.

DIMENSIONS OF HOLOTYPE. Length 1.51 cm, thickness 0.87 cm, width 1.29 cm ; this is the only specimen figured, B.M. BB.45161.

DESCRIPTION. *External characters.* The beak ridges and interarea are only weakly developed. The material was not sufficiently well preserved to allow the elucidation of the details of the pedicle opening and the deltidial plates. Concentric ornament was only observed on one specimen and consisted of growth lamellae.

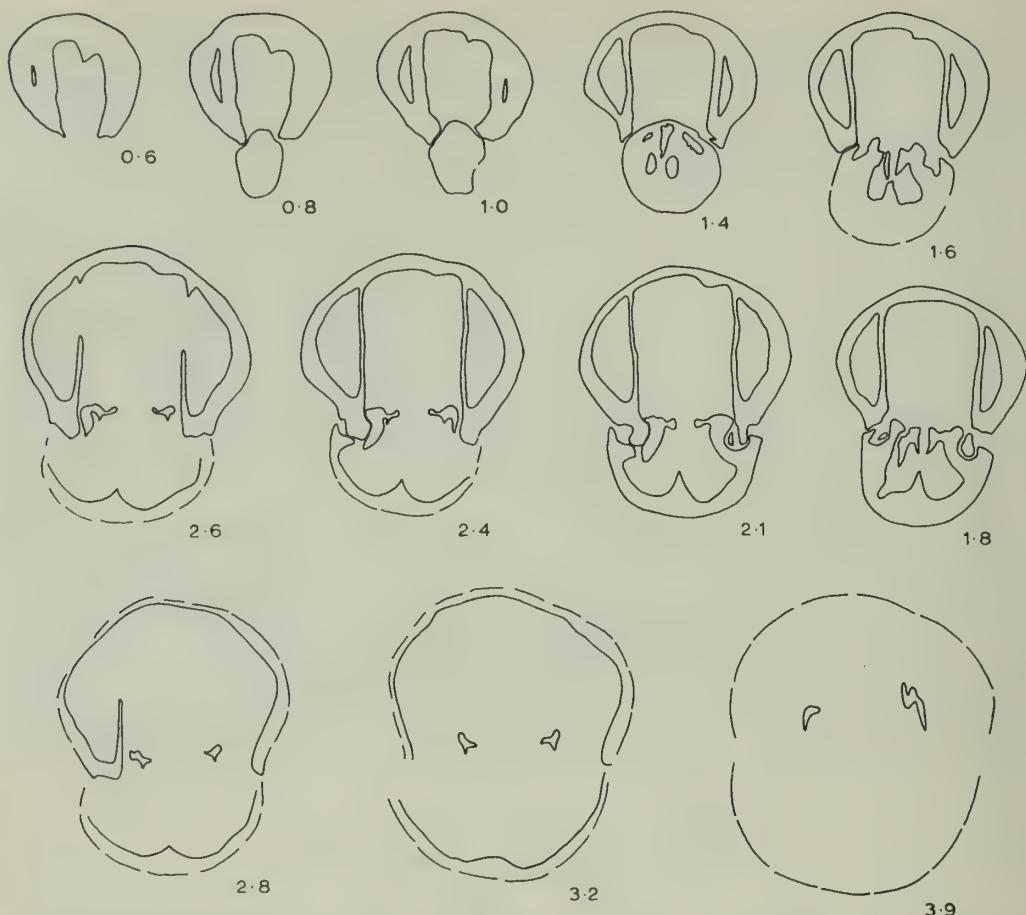


FIG. 40. Transverse serial sections of "*Rhynchonella*" *pyrenaei* sp. nov. Topotype. Oxfordian. Pic du Gar, (Basses Pyrénées), France. ($\times 5$).

Internal characters. *Pedicle valve.* The delthyrial cavity is subquadrate and limited by long, strong dental lamellae. Inner socket ridges are well developed; lateral denticulae are present.

Brachial valve. The median septum is strong and long septalial plates are developed. As seen in transverse section, the crura possess a very distinctive appearance through having "knob-like" structures median of the sharply pointed crural bases.

DISTRIBUTION. Only known from the type locality.

OCCURRENCE. All the material came from a bed about 10 cm thick where the species occurred profusely together with a lesser number of terebratulids. The matrix consisted of a very hard, dark limestone from which it was very difficult to extract specimens.

REMARKS. The species has not been referred to a genus as it is markedly dissimilar to any other species known to the author occurring in the Oxfordian. The distinctively shaped crura are closely comparable to those of *Prionorhynchia serrata* (J. de C. Sowerby) figured by Ager (1956); however, there is little resemblance externally and the latter is only known from the Lower Jurassic.

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PLATE I

All specimens are figured natural size.

In all cases: a=dorsal view. b=lateral view. c=anterior view. d=posterior view.

FIGS. 1 a-d. *Monticarella striocincta* (Quenstedt). Kimmeridgian—*cymodoce* zone. (Bedded Virieu Limestone), N. of Lac d'Armaille (Ain), France. Collection of the Geology Dept. of Imperial College, London.

FIGS. 2 a-d. *M. striocincta* (Quenstedt). Oxfordian ("Malm alpha"). Lochengründle, Germany. Collection of the University of Tübingen.

FIGS. 3 a-d. *M. striocincta* (Quenstedt). Details as fig. 2.

FIGS. 4 a-d. *Monticarella czenstochaviensis* (Roemer). Oxfordian. Holy Cross Mountains, Poland. Collection of Dr. D. V. Ager.

FIGS. 5 a-d. *Monticarella triloboides* (Quenstedt). Kimmeridgian, ("Weisser Jura delta"). "Schwäbische Alb". Collection of the University of Tübingen.

FIGS. 6 a-d, 7 a-d. *M. triloboides* (Quenstedt). Details as for fig. 5.

FIGS. 8 a-d. *Monticarella strioplicata* (Quenstedt). Kimmeridgian, ("Malm delta"). Barrenberg, Germany. B.M. BB. 44130.

FIGS. 9 a-d. *M. strioplicata* (Quenstedt). Details as fig. 8. B.M. BB. 44131.

FIGS. 10 a-d. *M. strioplicata* (Quenstedt). Details as fig. 8. B.M. BB. 44132.

FIGS. 11 a-d. *Lacunosella arolica* (Oppel). Oxfordian, *transversarium* zone. Jura meridionale, France. B.M. BB. 44134.

FIGS. 12 a-d. *L. arolica* (Oppel). Oxfordian, ("Birmensdorfer Schichten"), Birmensdorf, Switzerland. B.M. BB. 44133.

FIGS. 13 a-d. *Lacunosella pseudodecorata* (Roller). ?"Weis Jura gamma". ?Tüingen. Collection of the University of Tübingen.

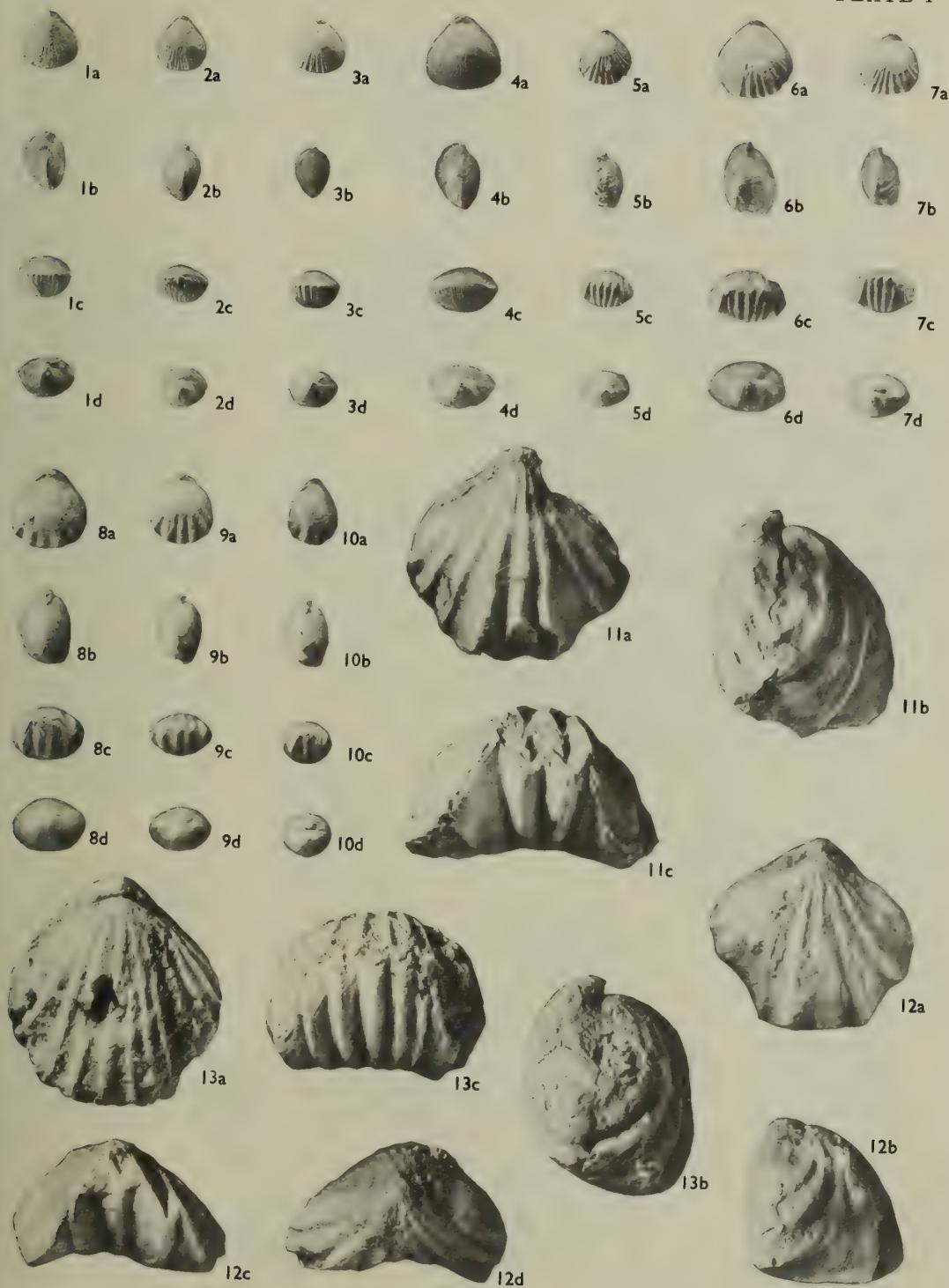


PLATE 2

Figs. 1 a-d. *Lacunosella vaga* sp. nov. Holotype. Kimmeridgian, *mutabilis* zone. Serméieu (Isère), France. B.M. BB. 44135.

Fig. 2. *L. vaga* sp. nov. Paratype. Details as fig. 1. B.M. BB. 44136.

Figs. 3 a-d. *L. vaga* sp. nov. Paratype. Kimmeridgian, ("Malm delta"). Lahm-Köttel, Germany. B.M. BB. 44137.

Figs. 4 a-d. *Lacunosella selliformis* (Lewiński). Oxfordian. Tokarnia near Checiny, Poland. B.M. BB. 44142.

Figs. 5 a-d. *Lacunosella cracoviensis* (Quenstedt). Upper Oxfordian-Lower Kimmeridgian, ("Malm beta/gamma"). Würgau, Germany. B.M. BB. 44138.

Figs. 6 a-d. *L. cracoviensis* (Quenstedt). Details as fig. 5. B.M. BB. 44139.

Figs. 7 a-d. *Lacunosella sparsicosta* (Quenstedt). Kimmeridgian, ("Malm gamma"). Barrenberg, Germany. B.M. BB. 44140.

Figs. 8 a-d. *L. sparsicosta* (Quenstedt). Details as fig. 7. B.M. BB. 44141.

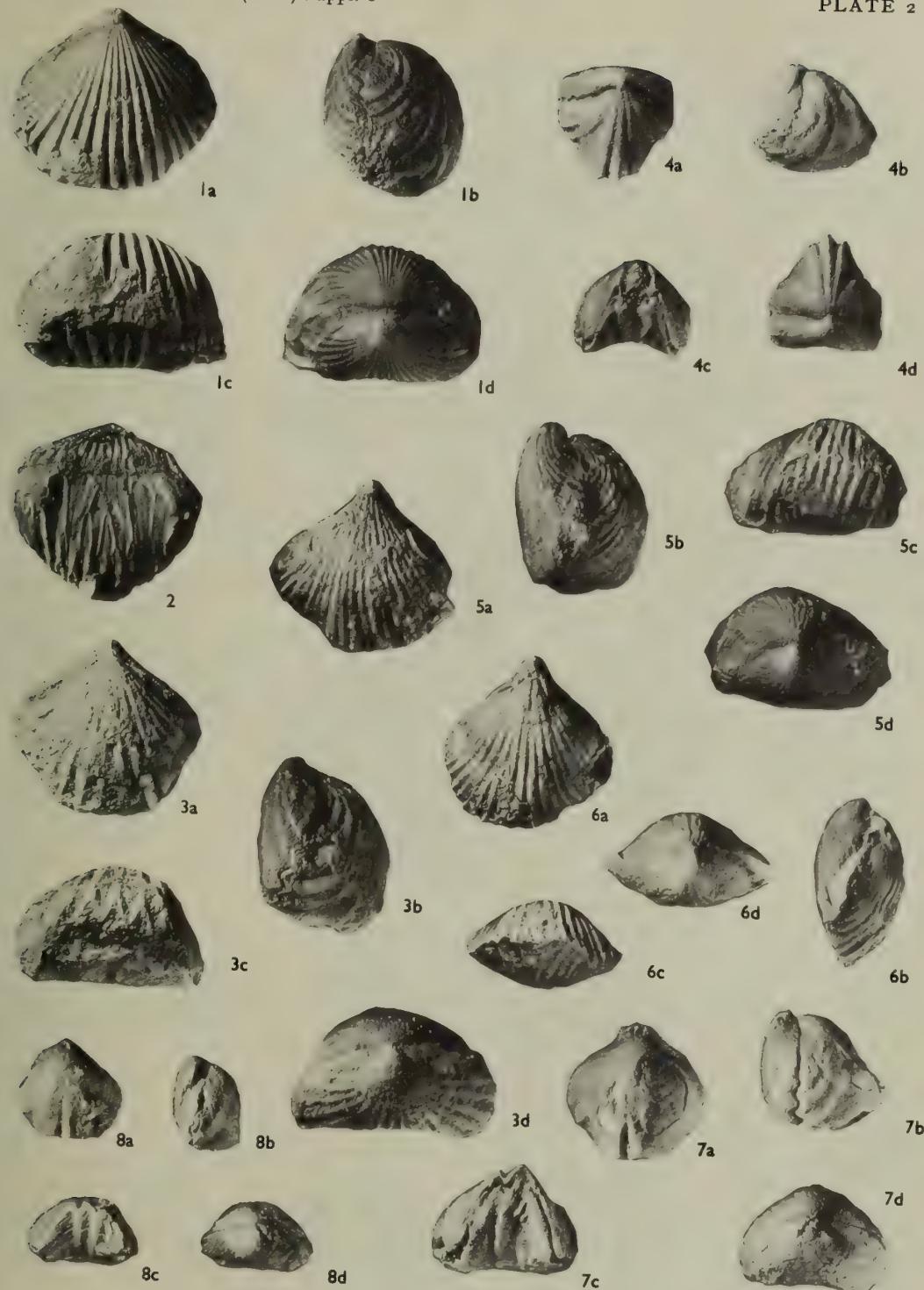


PLATE 3

FIGS. 1 a-d. *Lacunosella multiplicata* (Quenstedt). "Weiss Jura gamma". Thieringen, Germany. Collection of the University of Tübingen.

FIGS. 2 a-c. *Lacunosella trilobataeformis* Wiśniewska. "Malm alpha/beta". Rüsselbach bei Grafenberg, Germany. B.M. BB. 45160.

FIG. 3. *Lacunosella trilobata* (Zieten). Lower Volgian, ("Malm epsilon"). Wittislingen, Germany. B.M. BB. 44143.

FIGS. 4 a-d. *L. trilobata* (Zieten). "Kimmeridgien". Steinweiler bei Nattheim, Germany. Collection of the Naturhistorisches Museum, Basel. no. L 1691.

FIGS. 5 a-c, 6 a-d. *L. trilobata* (Zieten). Details as fig. 3. B.M. BB. 44144-5.

FIGS. 7 a-d. "*Rhynchonella*" *pyrenaei* sp. nov. Holotype. Oxfordian. Pic du Gar near Pau (Basses Pyrénées), France. B.M. BB. 45161.

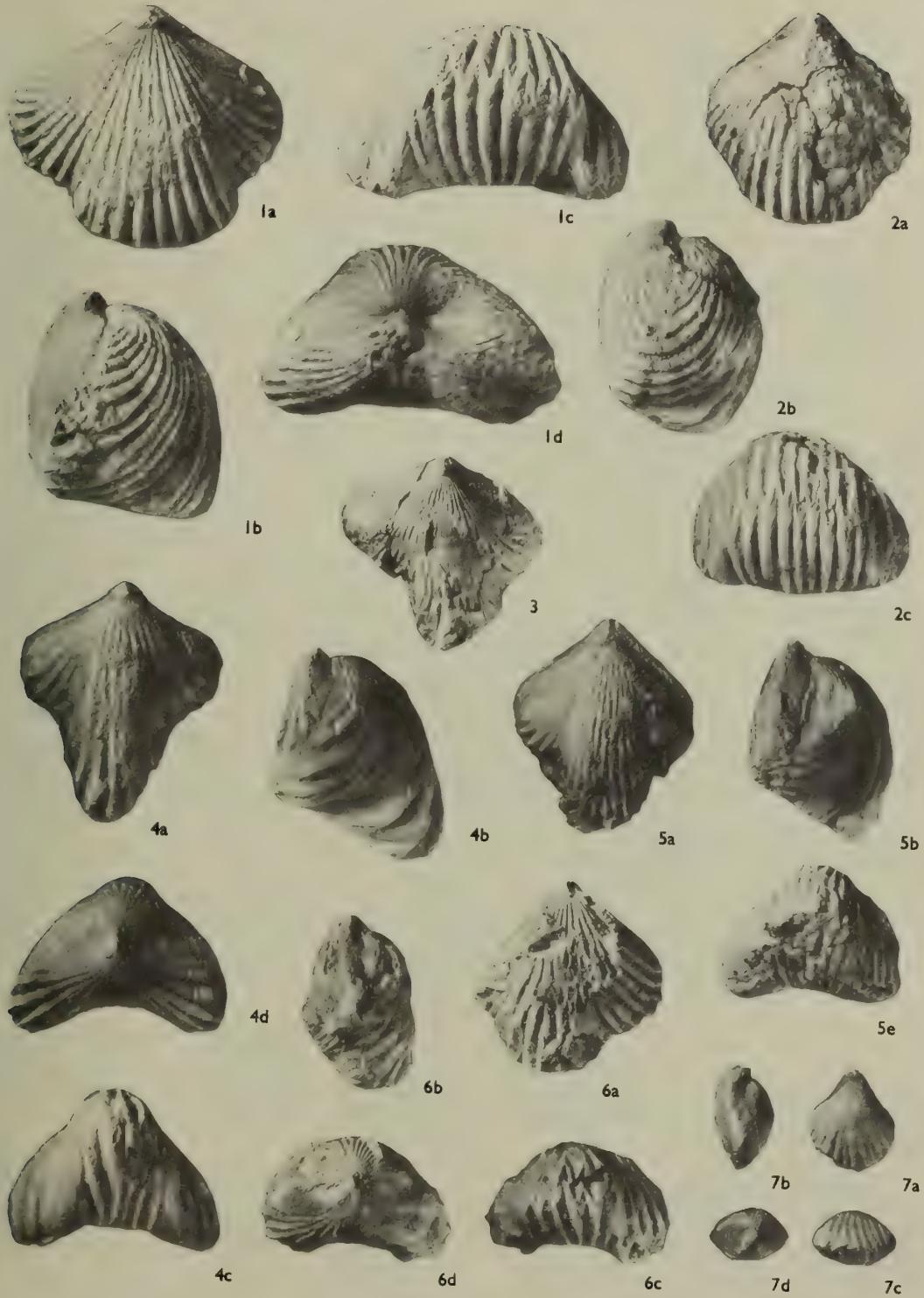


PLATE 4

Figs. 1 a-d. *Rhynchonella portlandica* Blake. Paratype. Lower Volgian, (Lower Portland Sand). St. Alban's Head, Dorset, England. B.M. B. 52284.

Figs. 2 a-d. *R. portlandica* Blake. Holotype. Details as fig. 1. B.M. B. 52283.

Figs. 3 a-d. *Rhynchonella loxiae* Fischer. Upper Volgian. Khoroshevo near Moscow. Collection of Dr. D. V. Ager.

Figs. 4 a-b. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Portland Sands). Ringstead Bay, Dorset, England. B.M. B. 72240.

Figs. 5 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Basal Shell Bed, Portland Limestone). Cliff N.W. of Portland, England. Collection of the University Museum, Oxford. J. 1006.

Figs. 6 a-d, 7, 8. *Rhynchonella* sp. Kimmeridgian, ?*pseudomutabilis* zone, (Boulder Beds), West Garty, Sutherland, Scotland. B.M. BB. 44146-7, 45162.

Figs. 9 a-c, 10 a-d, 11 a-d, 12 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Upper Blacknore Beds). West Weare Cliffs, Portland, England. Collection of the University Museum, Oxford. J. 2462.

Figs. 13 a-d, 14 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (upper part of Portland Sand). Foot of Gad Cliff, Dorset, England. Collection of the University Museum, Oxford. J. 167.

Figs. 15 a-d. *Rhynchonella* cf. *R. subvariabilis* Davidson. Lower Volgian, (top of Kimmeridge Clay just below Portland Sands Passage Beds). Chapman's Pool, Dorset, England. B.M. B. 47251.

Figs. 16 a-d. *Rhynchonella* cf. *R. subvariabilis* Davidson. Lower Volgian, (Kimmeridge Clay, about 40' below *rotundum* nodules). Chapman's Pool, Dorset, England. Collection of the Sedgewick Museum, Cambridge. J. 1500.

Figs. 17 a-d. *Rhynchonella* cf. *R. sarapaulensis* Makridin. Lower Volgian, (Kimmeridge Clay, rotundum nodules). Chapman's Pool, Dorset, England. Collection of the Sedgewick Museum, Cambridge. J. 1512.

Figs. 18 a-d. *Rhynchonella* cf. *R. portlandica* Blake. Lower Volgian, (Lyddite Bed, Portland Beds). Long Crendon, Buckinghamshire, England. Collection of the Sedgewick Museum, Cambridge. J. 1524.

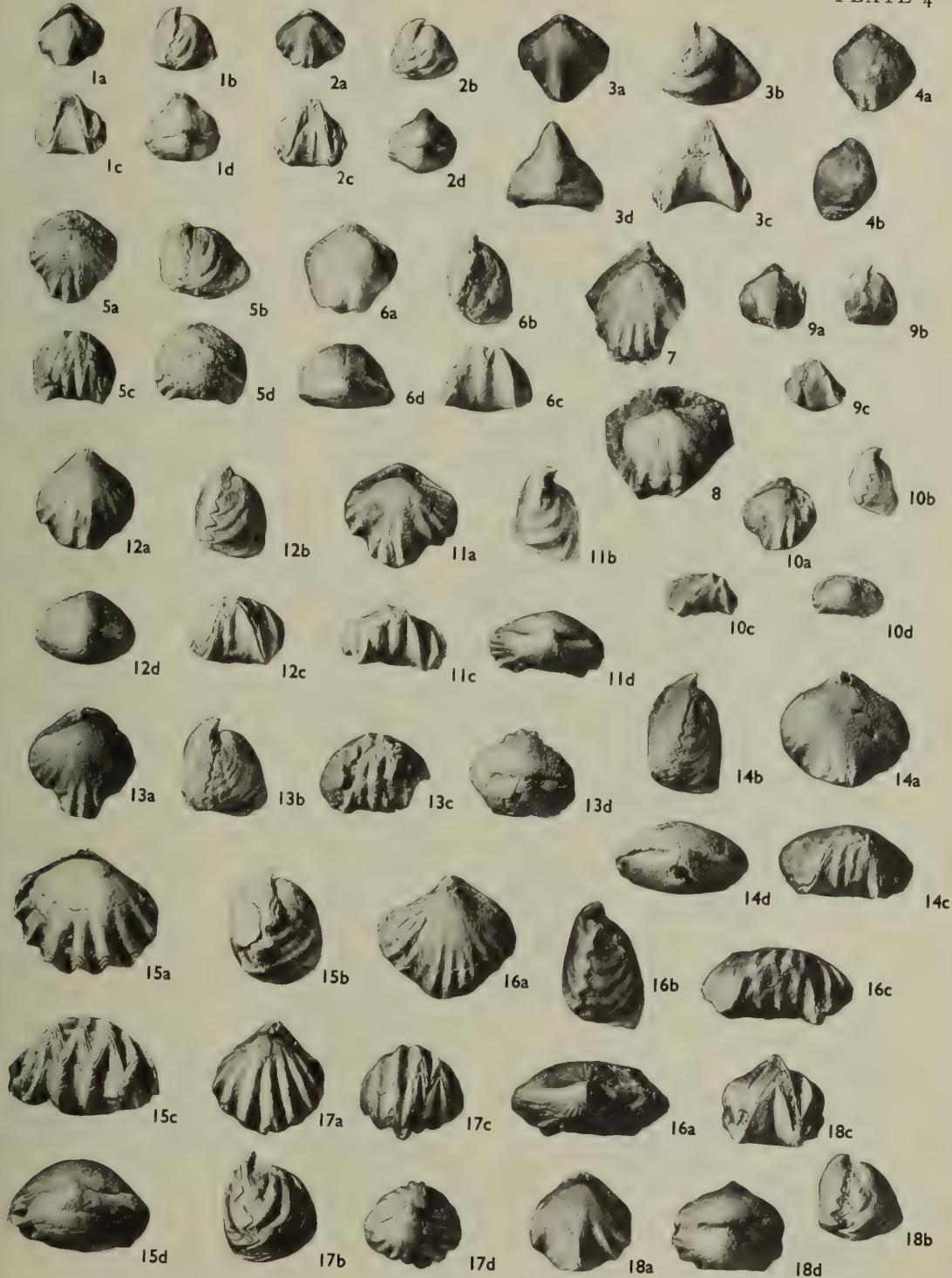


PLATE 5

FIGS. 1 a-d, 2 a-d. *Rhynchonella* sp. Callovian. Wrzova, Poland. B.M. BB. 44148-9.

FIGS. 3 a-d, 4 a-d, 5, 6. *Rhynchonella rivelensis* Loriol. Upper Oxfordian. Alex near Oyonnax (Ain), France. B.M. BB. 44150-53.

FIGS. 7 a-d, 8 a-d, 9 a-c. *Thurmannella obtrita* (Defrance). Oxfordian, (Terrain à Chailles). Pagny-sur-Meuse (Meurthe et Moselle), France. B.M. BB. 44154-56. Figs. 8 a-d neotype.

FIGS. 10 a-d. *Thurmanella acuticosta* sp. nov. Oxfordian, (Lower Calcareous Grit). Filey Brigg, Yorkshire, England. Holotype. B.M. BB. 44158.

FIGS. 11 a-d. *T. acuticosta* sp. nov. Paratype. Details as fig. 10. B.M. BB. 44157.

FIGS. 12 a-d. *Acanthothiris spinosa* (Linnaeus). Neotype. Bajocian, (Upper *Trigonia* or *Clypeus* Grit). Rodborough Hill, Gloucs., England. B.M. BB. 45400.

FIGS. 13 a-d. *A. spinosa* (Linnaeus). Bajocian, (Upper *Trigonia* or *Clypeus* Grit). Stroud, Gloucs., England. B.M. B. 63318.

FIGS. 14 a-d. *A. spinosa* (Linnaeus). Juvenile specimen. Bajocian, (Upper *Trigonia* Grit). Waterworks Quarry, Wotoon under Edge, Gloucs., England. B.M. BB. 44162.

FIG. 15. *A. spinosa* (Linnaeus). Crushed specimen showing spines attached. Upper Bathonian, ("Varians Schichten"). Liestal near Basel, Switzerland. B.M. BB. 44160.

FIGS. 16 a-d, 17 a-d. *A. spinosa* (Linnaeus). Details as fig. 15. B.M. BB. 44161 and 44159.

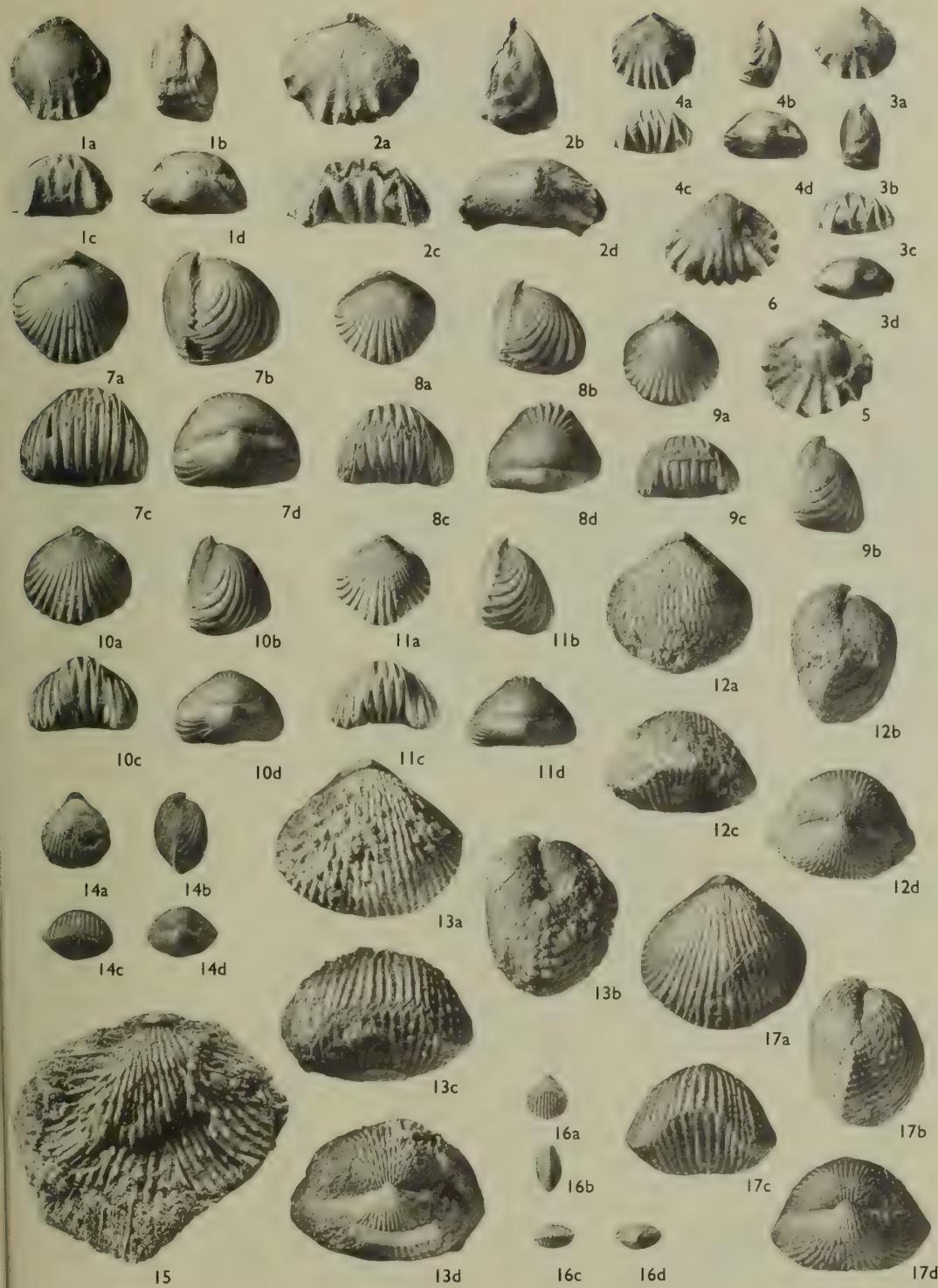


PLATE 6

FIGS. 1 a-d. Plaster cast of the type specimen Orbigny's *Acanthothiris costata* the original is in the collection of Jardin des Plantes (Musée d'histoire Naturelle), Paris. This specimen was figured by Thevenin (1910).

FIGS. 2 a-d, 3 a-d, 4 a-d. *Acanthothiris* cf. *A. costata* Orbigny. Upper Bajocian-Lower Callovian (Chanaz Beds). Pugieu (Ain), France. B.M. BB. 44163-65.

FIGS. 5 a-d. *Acanthorhynchia (Acanthorhynchia) panacanthina* (Buckman & Walker). Bajocian, zigzag zone. Burton Bradstock, Dorset, England. B.M. B. 63479.

FIGS. 6 a-d. *A. (Acanthorhynchia) panacanthina* (Buckman & Walker). "Inferior Oolite". Larkfield Quarry, Burton Bradstock, Dorset, England. B.M. B. 31306.

FIGS. 7 a-d. *A. (Acanthorhynchia) panacanthina* (Buckman & Walker). Bajocian, parkinsoni zone. Wennet Hills, Burton Bradstock, Dorset, England. B.M. B. 31304.

FIGS. 8 a-d. *Acanthorhynchia (Acanthorhynchia) spinulosa* (Oppel). "Oxfordien". Montsaon, Chaumont (Haute Marne), France. B.M. B. 36080.

FIGS. 9 a-d. *A. (Acanthorhynchia) spinulosa* (Oppel). "Oxfordien". Bolognes (Haute Marne), France. B.M. B. 36079.

FIGS. 10 a-d. *Acanthorhynchia (Acanthorhynchia) vilsensis* sp. nov. Paratype. Callovian. Legam bei Vils, southern Germany. Collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie, München. AS xxiv 5.

FIGS. 11 a-d. *A. (Acanthorhynchia) vilsensis* sp. nov. Holotype. Details as fig. 10. AS xxiv 2.

FIGS. 12 a-d. *A. (Acanthorhynchia) vilsensis* sp. nov. Paratype. Details as fig. 10. AS xxiv 5.

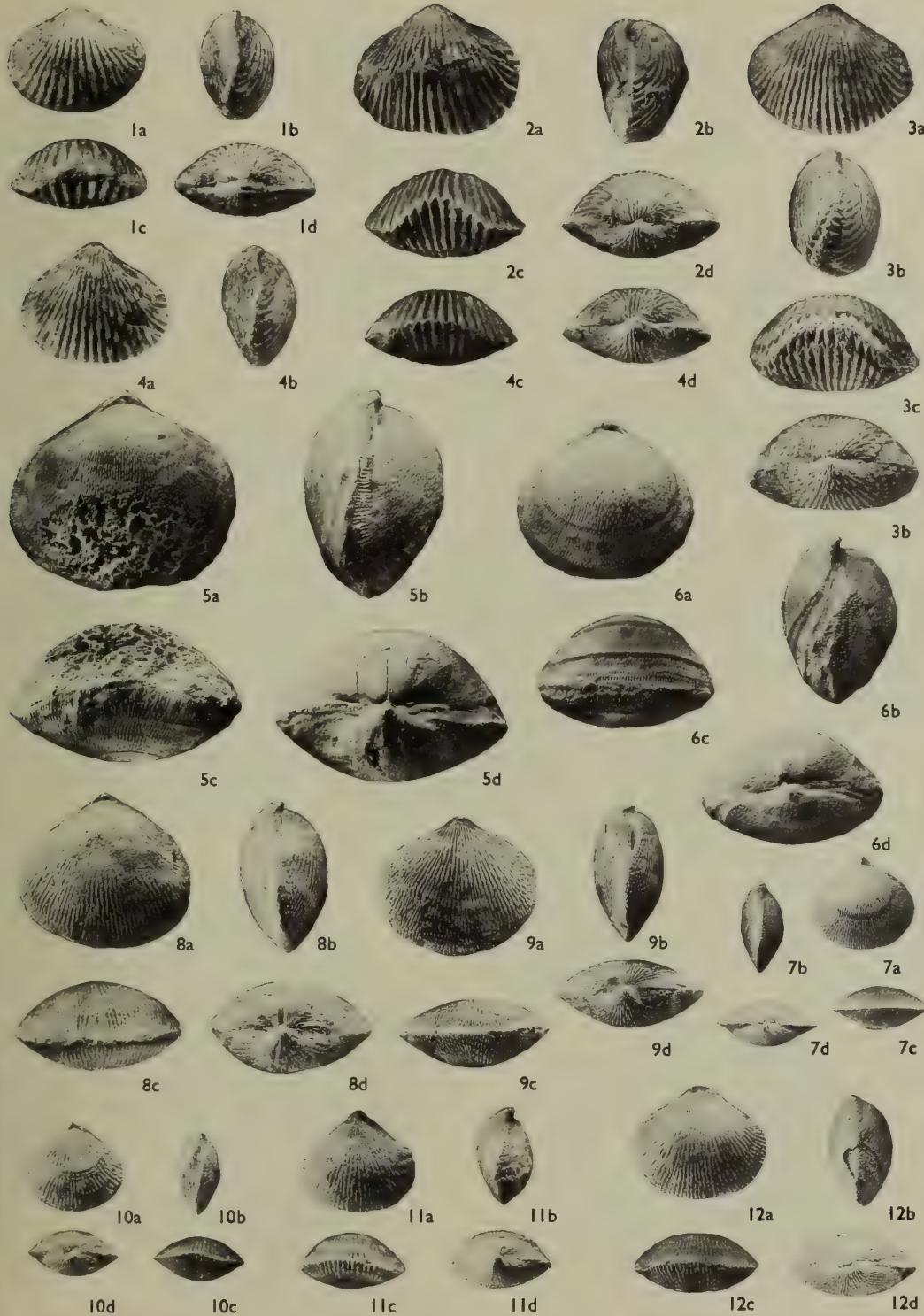


PLATE 7

FIGS. 1 a-d. *Acanthorhynchia (Echinirhynchia) senticosa* (Schlotheim). Neotype. "Weissem Jura". Amberg, Germany. Figured by Rothpletz (1886). Collection of the Bayerische Staatsammlung für Paläontologie und historische Geologie, München. AS vii 330.

FIGS. 2 a-d, 3 a-d. *A. (Echinirhynchia) senticosa* (Schlotheim). "Malm delta". Heiligenstadt near Erlangen, Germany. Collection of the Geologisches Institut der Universität, Erlangen.

FIGS. 4 a-d, 5, 6. *Acanthorhynchia (Echinirhynchia) fileyensis* (Buckman & Walker). Oxfordian, (Lower Calcareous Grit). Filey, Yorkshire, England. B.M. B. 31867, B. 31334, B. 31333.

FIGS. 7 a-d. *Acanthorhynchia (Echinirhynchia) lorioli* (Rollier). Oxfordian, (Terrain à Chailles). Fringeli, "Berner Jura". Collection of the Naturhistorisches Museum, Basel. L 1700.

FIGS. 8 a-d, 9. *A. (Echinirhynchia) lorioli* (Rollier). Oxfordian, *transverarium* zone. St. Sorlin, Liefnans (Jura), France. B.M. BB. 44166-67.

FIGS. 10 a-b, 11 a-d. *Acanthorhynchia* sp. Upper Kimmeridgian, (Oignon Limestone). Colomieu (Ain), France. B.M. BB. 44169, 44168.

FIGS. 12 a-d, 13, 14, 15, 16. *Somalirhynchia sutherlandi* (Davidson). Topotypes. Kimmeridgian, ?*pseudomutabilis* zone (Boulder Beds). West Garty, Sutherland, Scotland. Collection of the Geological Survey of Great Britain (Edinburgh Office). Fig. 12 no. G.S.E. 3684, West Garty; fig. 13 no. M 2268g, West Garty; fig. 14 no. G.S.E. 3681, West Garty; fig. 15 no. G.S.E. 3685, West Garty; fig. 16 no. G.S.E. 3686, Portgower.

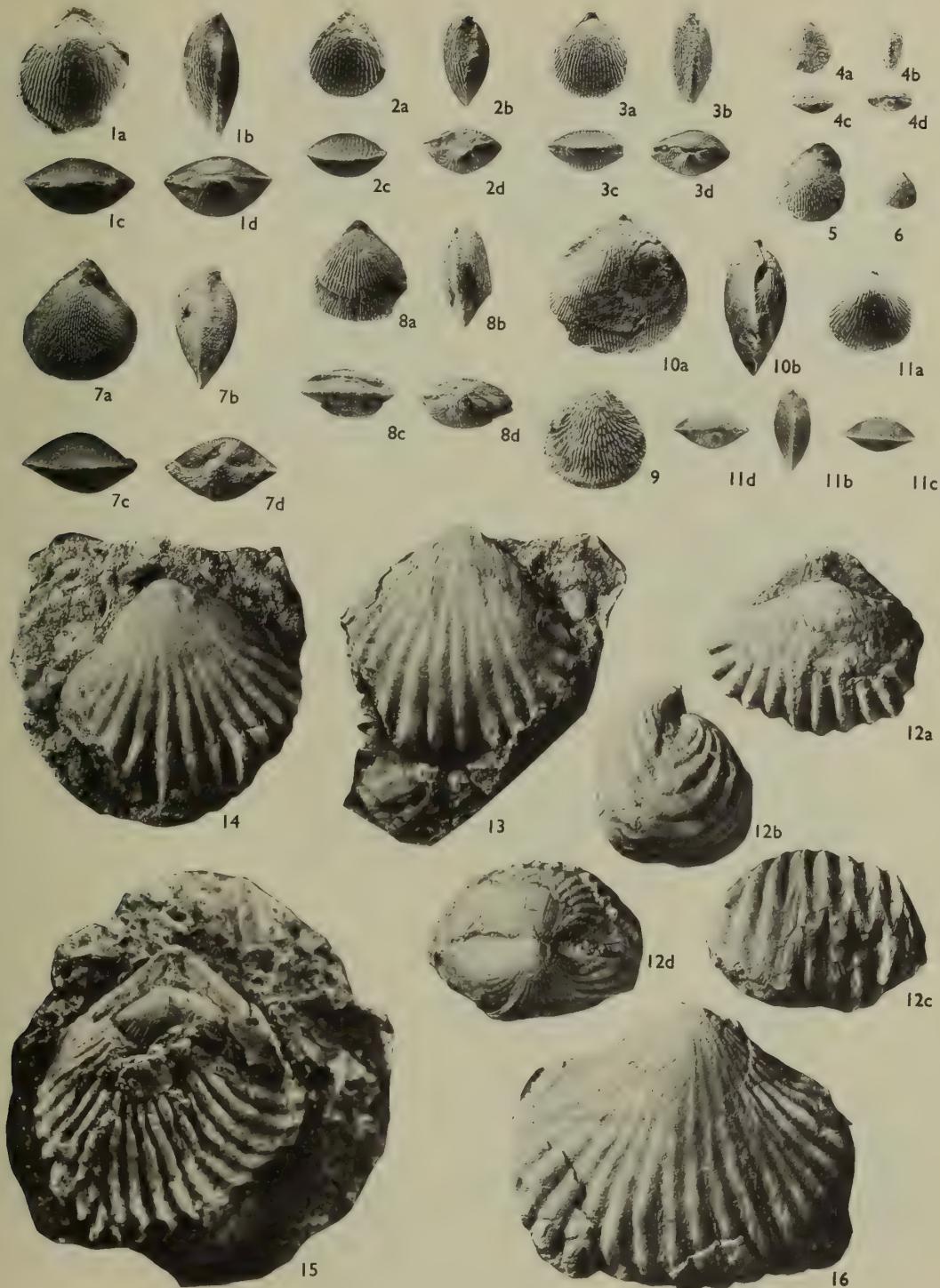


PLATE 8

FIGS. 1 a-d, 2 a-d, 3. *Somalirhynchia moeschi* (Haas). Oxfordian, *pseuaocordata* zone.
Rochers de Fresnois, Chaumont, près Saint-Claude (Jura), France. B.M. BB. 44170-72.

FIGS. 4 a-d, 5 a-d. *Septaliphoria arduennensis* (Oppel). Oxfordian, (Terrain à Chailles).
Pagny-sur-Meuse (Meurthe et Moselle), France. Fig. 4 neotype. B.M. BB. 44173-74.

FIGS. 6 a-d, 7 a-d. *Septaliphoria? septentrionalis* sp. nov. ?Upper Oxfordian-?lower
Kimmeridgian, (Alt-na-Cuile Sandstone). Alt-na-Cuile, Sutherland, Scotland. Fig. 6 holotype;
fig. 7 paratype. B.M. BB. 44175-76.

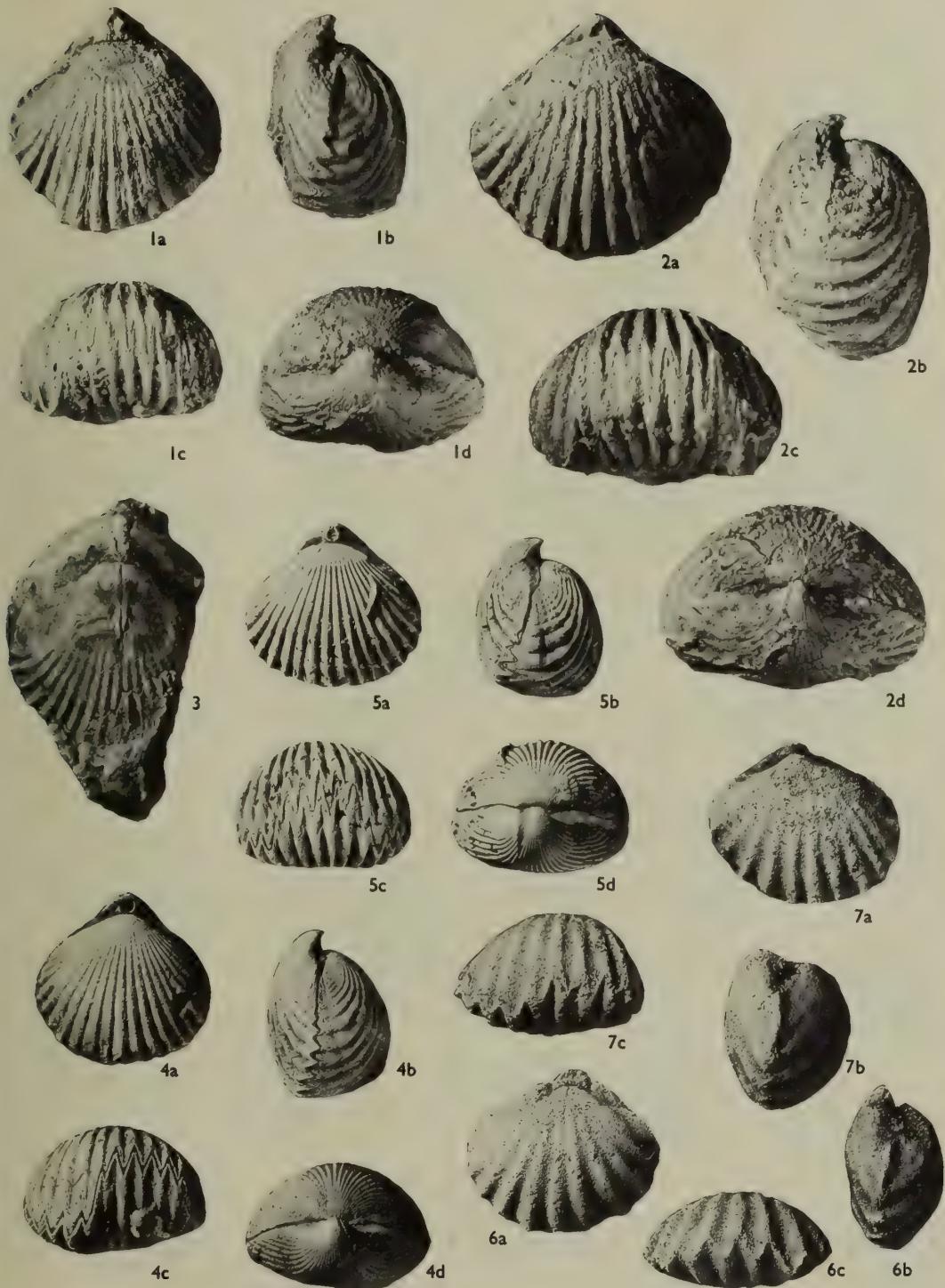


PLATE 9

Figs. 1 a-d, 2 a-c, 3 a-c, 4. *Septaliphoria? hudlestoni* (Rollier). Topotypes. Kimmeridgian, (Abbotsbury Ironstone). Abbotsbury, Dorset, England. B.M.

Figs. 5 a-c, 6 a-d. *Septaliphoria paucicosta* sp. nov. Oxfordian, (Lower Calcareous Grit). Hutton Bushell, Beedale, Yorkshire.

FIG. 5. Paratype; BB. 45395, fig. 6 holotype. B.M. BB. 45394.

Figs. 7 a-d, 8 a-d, 10, 11. " *Rhynchonella* " *ordinaria* sp. nov. Paratypes. " Sequanien ". Calliols du Chateau, Bourges (Cher), France. B.M. BB. 45163-66.

Figs. 9 a-d. " *Rhynchonella* " *ordinaria* sp. nov. Holotype. Oxfordian, *pseudocordata* zone. Mont Dolet, Sermétrieu (Isère), France. B.M. BB. 45167.

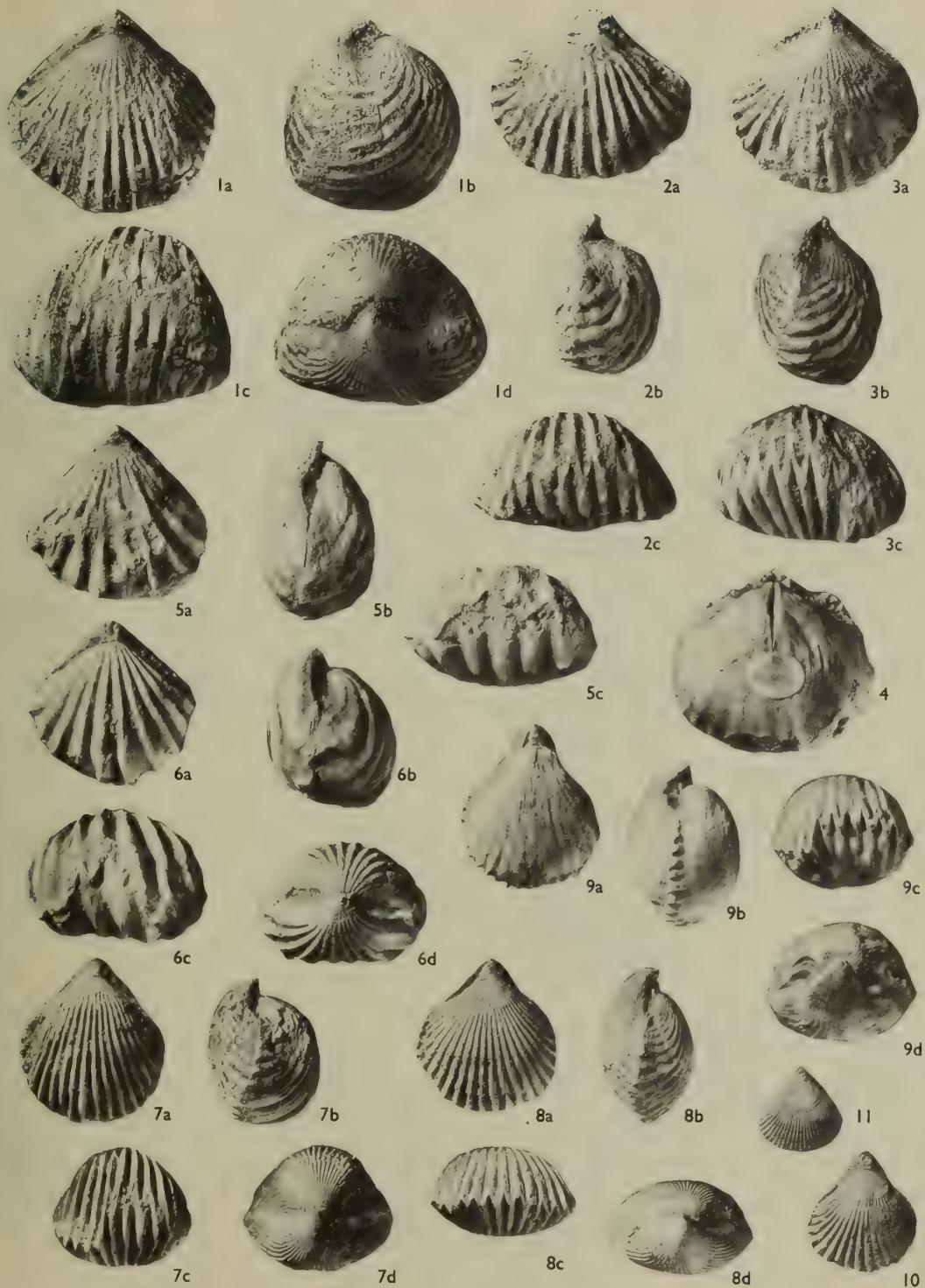


PLATE 10

Figs. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia inconstans* (J. Sowerby). Topotypes. Kimmeridgian, *baylei* zone, (Kimmeridge Clay). Ringstead Bay, Dorset, England. B.M. BB. 44177-79.

Figs. 4 a-c, 5 a-d, 6. *Torquirhynchia guebhardi* (Jacob & Fallot). Kimmeridgian, *cymodoce* zone, (Bedded Virieu Limestone). N. of Lac d'Armaille (Ain), France. B.M. BB. 45168-70.

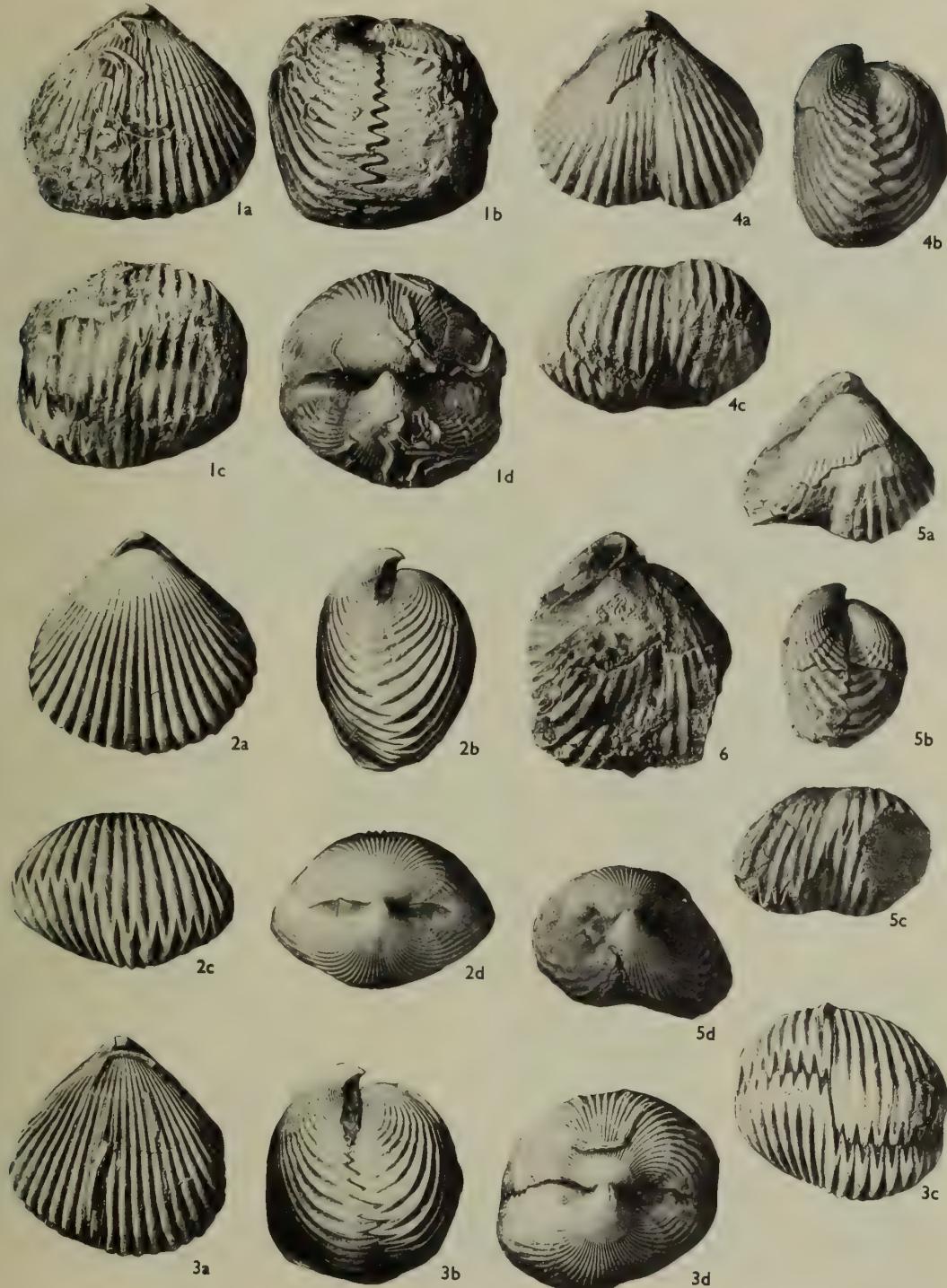


PLATE II

Figs. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia speciosa* (Münster). Upper Kimmeridgian-Lower Volgian ("Dieras-Kalk"). Saal near Ingolstadt, Germany. B.M. BB. 45171-73.



1a



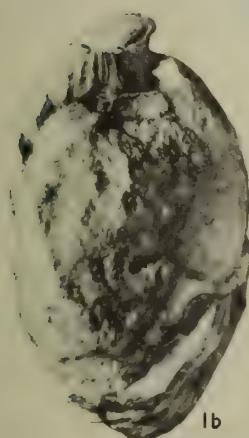
2a



1c



2d



1b



2b



2c



1d



3a



3d



3b

PLATE 12

FIGS. 1 a-d, 2 a-d, 3 a-d. *Torquirhynchia* cf. *T. astieriformis* (Wiśniewska). Kimmeridgian, *mutabilis* zone. Serméieu (Isère), France. B.M. BB. 45174-6.

FIG. 5. *Torquirhynchia inconstans* (Sowerby) from the Kimmeridge Clay of Ringstead Bay, Dorset. Shows the nature of the articulation, the shape of the median ridge and the outline of the muscle scars in the brachial valve. $\times 1\frac{1}{2}$. B. 60368.

FIG. 4. Transverse through the hinge plate of *Septaliphoria paucicosta* sp. nov. showing the form of the septalial plate and the crural base. This is part of section 4, 3 figured in text-fig. 33. $\times 12$.

FIG. 6. Transverse section of *Septaliphoria paucicosta* sp. nov. showing the median septum and septalial plates. This is part of section 3, 4 in the series shown in text-fig. 33. $\times 5$.

FIG. 7. Transverse section of *Acanthorhynchia (Acanthorhynchia) panacanthina* (Buckman & Walker) showing the thickened nature of the hinge plates. This is part of section 1, 9 in the series shown in text-fig. 24.

FIG. 8. Transverse section of *Zeilleria austriaca* (Zugmeyer) showing the form of the septalium. Specimen obtained from the Rhaetian of Piesting Tal, Lower Austria. The "peel" from which the photomicrograph was taken was kindly made available to the author by Dr. D. A. B. Pearson. $\times 5$.

FIG. 9. Transverse through the hinge plates of *Lacunosella vaga* sp. nov. showing the form of the falcifer crura. This is part of section 3, 6 in the series shown in text-fig. 14.



1a



1b



2a



2b



1c



1d



2c



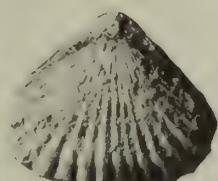
2d



4



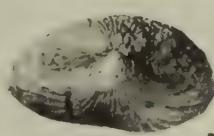
5



3a



3c



3d



6



7



8



9

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THE RELATIONSHIPS OF CERTAIN UPPER CRETACEOUS TELEOSTS WITH SPECIAL REFERENCE TO THE MYCTOPHOIDS

P. C. GOODY

THE RELATIONSHIPS OF CERTAIN UPPER CRETACEOUS TELEOSTS WITH SPECIAL REFERENCE TO THE MYCTOPHOIDES



BY
PETER C. GOODY

102 *Text-figures*

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By PETER C. GOODY

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SYNOPSIS

Redescriptions are given of most of the genera contained in Woodward's (1901) families Enchodontidae, Dercetidae and Scopelidae. Four new suborders are erected within the order Salmoniformes, the Ichthyotringoidei, Cimolichthyoidei, Enchodontoidei and Halecoidei. The Ichthyotringoidei contains two families, the Ichthyotringidae and the new family Apateopholidae. The Cimolichthyoidei contains the Dercetidae and the new family Cimolichthyidae, with a third new family appended, the Prionolepididae. The Enchodontoidei is composed of two families, Enchodontidae and the new family Eurypholidae. The Halecoidei contains the single family Halecidae. A new family Sardinoididae is added to the Myctophiformes and a new genus, *Pattersonichthys*, is included within the ctenothrissiform family Aulolepididae. Each group is discussed in relation to its systematic position and the information gained is used in an overall consideration of the evolution of the teleosts in the Cretaceous.

I. INTRODUCTION

THE present work is intended as a revision of certain lower teleostean fishes from the Upper Cretaceous. By the close of this era teleosts were numerous and varied and many of the present day suborders were represented, the notable exception being the perciform groups (see Patterson, 1967b). The faunal composition at the base of the Upper Cretaceous appears to have been almost as varied. Patterson (1964, 1967a) has dealt extensively with the Ctenothrissiformes and the acanthopterygian faunas from

the Upper Cretaceous, however teleosts below the acanthopterygian grade have received no modern comparable treatment, except for the work of Dunkle (1940) on the elopoid *Notelops brama*, and Bardack (1965) on the ichthyodectids.

The important earlier works on Cretaceous fish faunas are those of Agassiz (1833–1844), Heckel (1849), Pictet (1850), Pictet and Humbert (1866) and Davis (1887), and with the exception of Agassiz were all primarily concerned with material from the Lebanon. Dixon (1850) described forms from the English Chalk; von der Marck (1858, 1863) those from the Westphalian Chalk; and both Bassani (1882) and Kramberger (1895) considered the Dalmatian Chalk. The information contained in these and other earlier works was collected together and reinterpreted by Woodward (1901). The fish fauna of the English Chalk was later extensively treated in a monograph by Woodward (1902–1912). More recently d'Erasmo (1946) has worked on the Upper Cretaceous fauna from Comen near Trieste, Siegfried (1954) has reviewed von der Marck's Westphalian material, Arambourg (1954) has described a new fauna from Morocco, and Leonardi (1966) has reported on a Sicilian fauna.

Originally the work was begun as a revision of Woodward's (1901) family Enchodontidae. It was hoped that a study of the poorly known genera included in this family would yield possible ancestral forms for the present day Myctophiformes. This view had been expressed by Woodward (1901: ix) when he stated that "the Enchodontidae might perhaps furnish the ancestors" of the isospondylous scopeloids. All of the genera in the family have been considered and most are described at some length in the following pages. Only those species represented by reasonably complete material have been included, species erected on isolated teeth or jaw fragments are omitted. The Upper Cretaceous fauna of the United States has not been treated due to the absence of good material in collections outside America.

During the study of the Enchodontidae it soon became clear that many of the included genera were not at all closely related. In order to elucidate the systematic position of some of these genera it was necessary to consider two more of Woodward's (1901) families, the Dercetidae and Scopelidae. Many of the genera were found to be not only widely separated, but referable to different suborders and even orders. Consequently recent representatives of the orders Elopiformes, Salmoniformes and Myctophiformes have also been studied.

The first part of the work is devoted to the detailed description of the fossil genera, and is set out in sequence from the most primitive Salmoniformes up through the Myctophiformes to the Ctenothrissiformes. The findings concerned with the Elopiformes have been published elsewhere (Goody, 1969). In the second part, each of these major fossil groups is considered in relation to its systematic position, while certain morphological problems and possible modes of life are also discussed. Thirdly the information set out in the first two parts is used in an overall consideration of teleost evolution within the Cretaceous.

Most of the fossil material used is from the collections in the British Museum (Natural History), referred to, throughout this work, as the B.M.N.H. Type material has been examined wherever possible and certain specimens have been loaned from museums in Europe. Where such material has been examined, mention is made in the text.

Preparation of fossil material was mainly accomplished by dissolving the matrix in acetic acid (Toombs, 1948; Rixon, 1949). Specimens 'in the round' were immersed in 2% to 5% acetic acid, for periods of several hours, after which they were washed in running water and then thoroughly dried. The subsequently exposed bone was hardened by the application of a solution of Vinalak 5917 in methyl ethyl ketone. The Vinalak was most effective when used in low concentrations. In two cases, where the material had previously been figured, a replica of the original was obtained by making silicone rubber moulds which were employed for the production of plaster of paris casts.

Acid preparation was also used in conjunction with the embedding of flattened specimens in a cold-curing polyester resin, Crystic 195, the transfer method of Toombs and Rixon (1950). Excellent preparations of specimens from the Middle Cenomanian deposits of Hakel and Hajula in the Lebanon were obtained by this method. The matrix in this case is a much harder, more fissile limestone than is the English Chalk and greater concentrations of acetic acid, up to 20%, were used.

The recent material used was either skeletal or alizarin preparations. In the case of the Myctophiformes the specimens from which bone and alizarin preparations were made were kindly loaned by Dr. G. Maul of Funchal in Madeira.

Certain teleost bones have been given varying names throughout the literature. The nomenclature adopted in this work agrees with that of Patterson (1964), with the addition that the caudal skeleton terminology follows that of Nybelin (1963). In the systematic descriptions the vertebral counts always exclude the ural vertebrae and any preural vertebrae to which these may fuse, thus the count extends to the first free preural vertebra. Also in the systematic descriptions caudal vertebrae are those vertebrae which possess a complete haemal arch. Finally the classification adopted is that proposed by Greenwood, *et al.* (1966).

II. SYSTEMATIC DESCRIPTIONS

Superorder PROTACANTHOPTERYGII

Order SALMONIFORMES

Suborder ICHTHYOTRINGOIDEI

DIAGNOSIS. Head elongated anteriorly into a prominent rostrum ; body short. Maxilla enters gape, toothed or untoothed. Teeth on premaxillae, palatines, ectopterygoid, endopterygoid and dentary ; vomer untoothed. 9 branchiostegal rays. Pectoral fins with up to 20 rays, low on flanks ; mesocoracoid arch present ; pectoral girdle with 2 postcleithra. Epineurals along most of the body. Anterior neural spines consist of separate lateral elements. Caudal skeleton with 2 free ural vertebrae ; 19 principal rays of which 17 are branched. Fins without spines. Scales cycloid.

Family ICHTHYOTRINGIDAE Jordan, 1905

DIAGNOSIS. Head excessively elongated and shallow; body unelongated. Post-temporal fossa roofed. Parietals meet in the mid-line. Orbitosphenoid and basiphenoid present. Posterior infraorbital bones expanded. Mandibular suspensorium vertical or near vertical. Preoperculum with no ventral spine. Vertebral elements relatively well fused; centra longer than deep. Body covered with thin cycloid scales enlarged along the lateral line. Dermal bones smooth, devoid of ornamentation.

Genus **ICHTHYOTRINGA** Cope, 1878

DIAGNOSIS (emended). Ichthyotringidae in which the head is very shallow and elongated. Dermal bones of the head smooth and unornamented. Jaw suspension vertical or inclined very slightly forwards. Branchiostegal rays approximately 9 in number. Vertebrae 40 in number, of which 17 are caudal. Individual centra longer than deep. Pectoral fin with up to 20 rays. Pelvic fins abdominal with as many as 12 rays.

TYPE SPECIES. *Ichthyotringa tenuirostris* Cope.

REMARKS. Cope's generic name *Ichthyotringa* (1878:69) replaces *Rhinellus* Agassiz (1844 : 260) which is preoccupied.

***Ichthyotringa furcata* (Agassiz)**

(Text-figs. 1-4)

- 1844 *Rhinellus furcatus* Agassiz, 2 : 260, pl. 58b, fig. 5.
- 1849 *Rhinellus furcatus* Agassiz; Heckel : 340, pl. 23, fig. 1b.
- 1850 *Rhinellus furcatus* Agassiz; Pictet : 44, pl. 8, figs. 3, 4.
- 1866 *Rhinellus furcatus* Agassiz; Pictet & Humbert : 82, pl. 11, figs. 5-8.
- 1873 *Rhinellus furcatus* Agassiz; von der Marck : 60, pl. 2, fig. 4.
- 1887 *Rhinellus furcatus* Agassiz; Davis : 608.
- 1901 *Rhinellus furcatus* Agassiz; Woodward : 266, pl. 13, figs. 1, 2.
- 1908 *Rhinellus furcatus* Agassiz; Priem : 10, pl. 1, fig. 13.
- 1932 *Rhinellus furcatus* Agassiz; Woodward : 162, fig. 249.
- 1954 *Rhinellus furcatus* Agassiz; Siegfried : 21.
- 1964 *Ichthyotringa furcata* (Agassiz) Danil'chenko : 418, fig. 140.
- 1966 *Rhinellus furcatus* Agassiz; Lehman : 203, fig. 201.

DIAGNOSIS (emended). *Ichthyotringa* of standard length not exceeding 10 cm. Head with opercular apparatus occupies half the standard length. Mandibular suspensorium vertical. Dorsal fin with 12 rays, mid-way between occiput and caudal peduncle. Anal fin with 15 rays arising behind dorsal fin, nearer to caudal than to pelvics. Pelvics in advance of dorsal fin with 11 rays. Vertebral column with 40 vertebrae.

HOLOTYPE. Present location unknown to the author, at one time in the Amic collection in Paris. The holotype was from the Upper Senonian of Sahel Alma, Lebanon.

MATERIAL. B.M.N.H. numbers 48089a, 48089b, 48092, 49544, all from the Upper Senonian of Sahel Alma, Lebanon, and all prepared by the transfer method in acetic acid. Specimen number 8436, being the negative impression of a complete fish in the Paläontologisches Institut der Westfälische Wilhelms-Universität, Münster. This latter specimen was that used by von der Marck (1873 : 60, pl. 2, fig. 4), and is from the Upper Senonian of Sendenhorst, Westphalia.

DESCRIPTION. *Neurocranium*. A dorsal view of the reconstructed neurocranium is shown in Text-figure 1. The neurocranium is elongate, shallow, relatively narrow, and drawn out preorbitally to enter into the composition of the rostral region. The mesethmoid extends the whole length of the rostrum and so too does the vomer below it. In the base of the orbit the parasphenoid contacts the vomer anteriorly in front of the lateral ethmoids. The frontals form most of the skull-roof and are unornamented, but bear two large lateral ridges which run longitudinally above the orbital region and demarcate a median interorbital depression. Lateral to the ridges, above the orbit, the frontals are curved, forming the upper margin to the orbit.

The supraoccipital is small and contacts the parietals anteriorly and the epiotics laterally. The parietals are large and meet in the mid-line of the skull-roof anterior to the supraoccipital. Laterally the parietals curve ventro-laterally and are overlapped by the pterotics, forming, presumably, the roof of the post-temporal fossa.

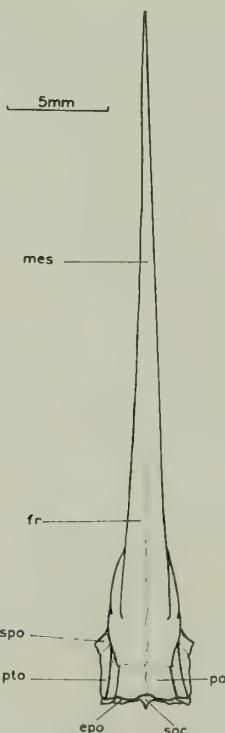


FIG. 1. *Ichthyotringa furcata* (Agassiz). Neurocranium in dorsal view.

The sphenotic makes up the postero-dorsal corner of the orbit, contacting the pterotic posteriorly and the frontal dorso-medially. The pterotic forms the postero-lateral border of the skull-roof and is inclined ventro-laterally. The anterior region of the hyomandibular facet is composed of sphenotic with the possibility of a contribution from the prootic, while the main part of the facet is formed from pterotic. The epiotics form the postero-lateral region of the occipital border of the roof bounding the parietals posteriorly. The dorsal region of the epiotic is thickened to produce a knob of bone with which the dorsal limb of the post-temporal articulated.

Within the posterior region of the orbit, traces of median bony elements are observable which may correspond to an orbitosphenoid and a basisphenoid, but may simply be other neurocranial bones which have become displaced.

Jaws and suspensorium. The dermal upper jaw is extended into a long thin rostrum, with contributions from the palate and neurocranium. The hyomandibular has an elongated head with a lateral crest passing back to the rear edge of the bone. The hyomandibular is held vertically and the quadrate condyle is immediately below the occiput. The quadrate is a shallow, triangular bone with an expanded and extremely well ossified ventral condyle. The condyle is transversely orientated and fits into a shallow articular facet. The quadrate meets the ectopterygoid anteriorly and the metapterygoid dorsally. The metapterygoid is clearly visible overlapping the anterior regions of the lateral face of the hyomandibular. The anterior edge of the metapterygoid is produced into an oblique thickened ridge which is continuous with a ridge on the postero-dorsal part of the ectopterygoid. The ectopterygoid is thin and elongated, posteriorly contacting the quadrate and the metapterygoid, and anteriorly the palatine. The connection with the palatine is in the region of the lateral ethmoid at the anterior end of the orbit. The palatine continues forwards as a direct extension of the ectopterygoid along the entire length of the rostrum. The palatine bone is supported medially by the extended mesethmoid and vomer and takes the form of a thin vertical lamina of bone. Its ventral edge bears a single row of relatively large, slightly recurved needle-like teeth.

The dermal upper jaw is composed of premaxilla and maxilla, although it is practically impossible to determine to what extent the maxilla enters the oral border. It would appear that at least the anterior two-thirds of the gape is produced by the premaxilla and possibly more. The dermal upper jaw bears a marginal row of minute teeth.

The mandible is long and shallow bearing two rows of teeth, a marginal row of minute teeth and an inner row of larger teeth approaching the size and form of those on the palatine. Almost all of the mandible is composed of dentary, the articular being a relatively small component. The articular facet is shallow, despite the size of the quadrate condyle, and there is no coronoid or retroarticular process.

Opercular bones. The preoperculum is narrow and upright with a slight basal expansion. The anterior edge of the preoperculum abuts against the posterior face of the hyomandibular crest dorsally, and against the rear edge of the quadrate ventrally. The operculum is large, slightly deeper than it is long with a rounded upper and posterior margin and a straighter, postero-dorsally inclined ventral edge. The suboperculum is large with rounded ventral and posterior edges. Dorsally it is

attached to the internal face of the operculum. A small interoperculum appears to be present, below the suboperculum and near to the ventral preopercular region. The opercular bones are smooth, as are the other dermal skull bones.

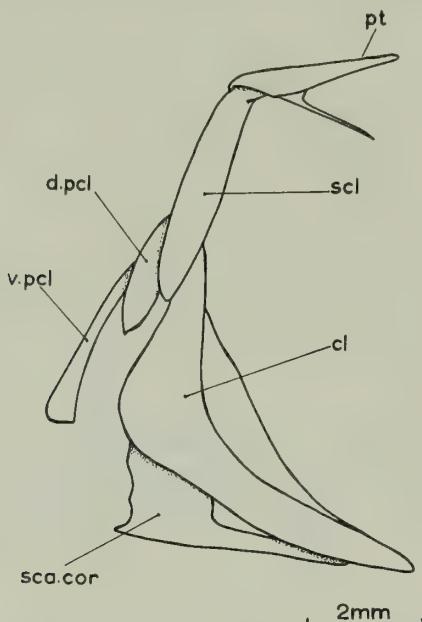


FIG. 2. *Ichthyotringa furcata* (Agassiz). Pectoral girdle of the right side in lateral view.

Paired fins and girdles. The pectoral girdle is shown in lateral view in Text-figure 2. The post-temporal bears a flattened narrow dorsal limb in association with the occipital region of the skull. The supracleithrum articulates with the postero-medial region of the post-temporal, and is a short but expanded bone inclined slightly backwards ventrally. The cleithrum is a large curved bone, whose anterior edge is turned medially to form the posterior border to the branchial opening. Two post-cleithra are present, attached to the posterior region of the supracleithrum and cleithrum. The dorsal postcleithrum is oval in shape, but the ventral postcleithrum is thinner and more elongated. The endoskeletal girdle is indistinct. The coracoid, however, is expanded where it curves forwards to connect with the tip of the cleithrum. The pectoral fin articulates with the posterior edge of the endoskeletal girdle through the intermediary of four hour-glass shaped radials. The pectoral fins are large and appear to have a variable number of fin rays, between 16 and 20. The rays are segmented and bifurcated distally.

The pelvic girdle consists of a pair of elongated triangular bones lying in the mid-ventral region of the body wall. The bones contact each other at their extreme anterior ends and posteriorly by medial bony processes behind the fin insertion, this being in advance of the origin of the dorsal fin. Each fin consists of approximately 11 rays, similar in form to those of the pectoral.

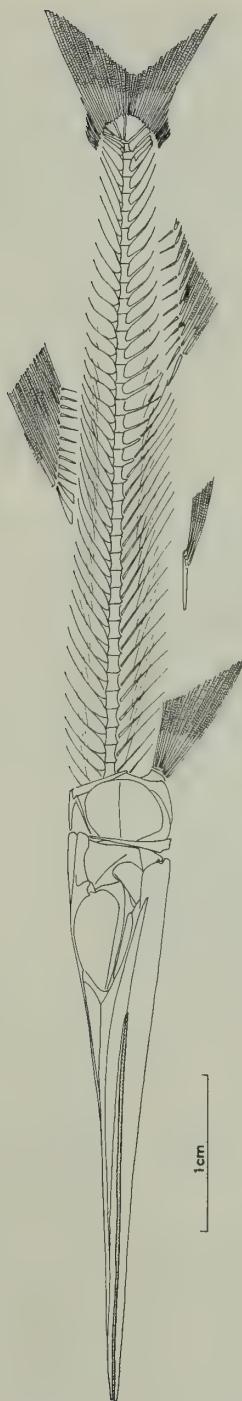


FIG. 3. *Ichthyotringa furcata* (Agassiz). Restoration of the skeleton, scales omitted.

Vertebral column. The entire vertebral column is shown in the restoration of the skeleton (Text-fig. 3). It consists of 40 vertebrae of which approximately 23 are precaudal and 17 caudal. The centra are slightly longer than they are deep and are considerably mesially constricted. Laterally the centra bear about three longitudinal raised ridges, but more posteriorly in the caudal region the lateral ridges are reduced to two. In the precaudal region neural spines are very fine and long with a prominent backward curvature, but in the caudal region the spines become shorter, stouter and straighter. All of the neural arches are intimately connected to the corresponding centra. The precaudal vertebrae bear small antero-ventral transverse processes with which pleural ribs articulate. The ribs are long, thin and strongly curved both posteriorly and ventrally around the body cavity. The enlargement and ventral prolongation of the transverse processes begins at about the 20th precaudal vertebra and fusion occurs by the 24th vertebra. The haemal arches thus produced gradually become drawn out into backwardly projecting haemal spines. Prezygapophyses and postzygapophyses are not prominent on the precaudal vertebrae but are more apparent caudally.

Intermuscular bones, both epineurals and epipleurals, occur on the first 33 vertebrae. Anteriorly the epineurals articulate with the neural arches, but more posteriorly the region of attachment rises on to the neural spines. Epipleurals anteriorly are associated with the centra, but in the caudal region associate with the haemal arches and spines.

Median fins and tail. The fins are shown in the restoration of the whole skeleton (Text-fig. 3). The dorsal fin is made up of approximately 13 rays and is situated about mid-way between the occiput and the base of the caudal fin. The first ray is short and unbranched unlike the remainder which are longer and branched. All of the fin-rays are segmented. The proximal radials are long and thin with expanded head regions. The anteriormost radial has an expanded shaft region which bears a median anterior keel-like expansion. The distal ends of the proximal radials are expanded antero-posteriorly and inclined at a slight angle to the long axis of the fin; this is probably due to the fusion of the medial radials to the proximal radials.

The anal fin is composed of 15 rays, situated behind the level of the posterior end of the dorsal fin. None of the proximal radials are expanded, all are thin and rod-like with only slightly expanded heads. The first ray is short and unbranched, the remainder are longer and branched.

The caudal skeleton (Text-fig. 4) consists of six vertebrae, four preural vertebrae and two ural vertebrae, the second ural merely being a terminal half-centrum. Preural vertebrae 2, 3 and 4 all bear prominent neural and haemal spines which project more noticeably backwards than the spines of the vertebrae preceding them. The spines of these three preural vertebrae support the small accessory rays of the caudal fin. The first preural centrum is reduced in length and inclined slightly postero-dorsally. The haemal spine of preural 1 (the parhypural) is prominent and expanded. Dorsally the first preural vertebra does not bear a neural spine, simply an enlarged neural arch. The first ural vertebra is even more reduced in extent than the first preural vertebra and is upturned. On its ventral edge the first ural vertebra bears two expanded hypurals which extend to the mid-line of the caudal fin. Ural

vertebra 2 is a small fraction of a centrum bearing the upper four hypurals. Associated with the dorsal and lateral regions of the first preural vertebra and both ural vertebrae, are several uroneural elements which are long and thin and inclined postero-dorsally. The first uroneural, which is clearly associated with preural vertebra 1 and ural vertebra 1, bears a median anterior expansion. This expansion extends anteriorly above the neural arch of the first preural vertebra towards the neural spine of the second preural vertebra. With the dorsal region of this uroneural expansion at least two epurals are associated.

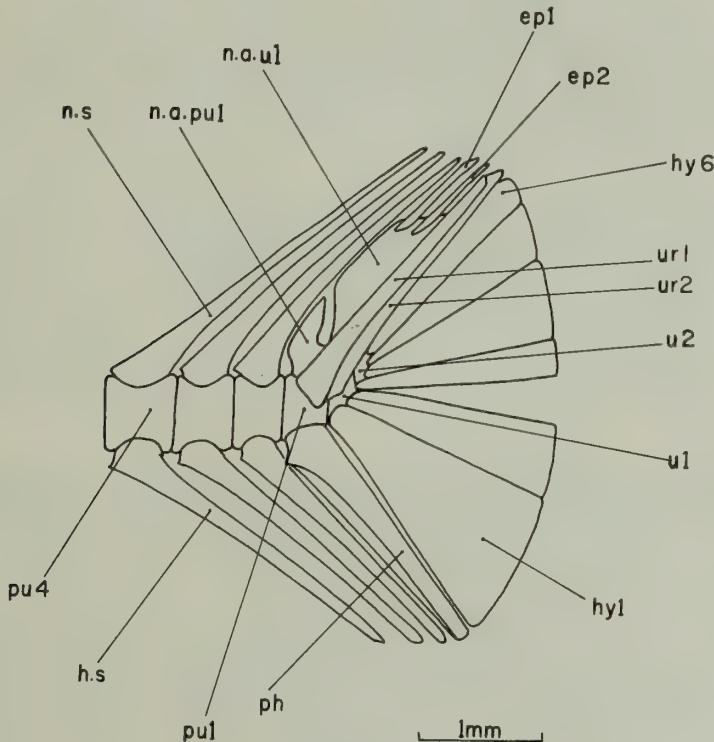


FIG. 4. *Ichthyotringa furcata* (Agassiz). Caudal fin skeleton in lateral view.

The caudal fin is composed of 19 principal rays of which 17 are branched. The accessory rays are shorter and unbranched and occur both above and below the caudal peduncle, there being 16 accessory rays in all.

Scales. The whole body is covered with small cycloid scales, all of which are marked with concentric ridges. The scales along the course of the lateral line are noticeably different, being squarer in outline and bearing a longitudinal raised ridge.

Ichthyotringa delicata (Hay)

(Text-fig. 5)

1903 *Rhinellus delicatus* Hay : 432.

DIAGNOSIS. *Ichthyotringa* of estimated standard length 30 mm. Head shallow with a flattened roof. Mandibular articulation lying below the orbit. Preoperculum expanded antero-ventrally but with posterior edge remaining vertical. Vertebral column consisting of 43 vertebrae.

HOLOTYPE. Specimen number 4530 in the American Museum of Natural History, from the Middle Cenomanian of Hajula in the Lebanon.

MATERIAL. B.M.N.H. specimen number P.48831. This specimen was obtained during the transfer development of further specimens of a different genus. P.48831 is a small, fragmentary, flattened specimen entirely dissociated from the matrix. The snout region is absent and the body is broken and incomplete but the skull-roof is intact up to the anterior end of the orbits.

REMARKS. Due to the fragmentary nature of the specimen a complete description is not available, but those features which are observable warrant its reception in the genus *Ichthyotringa*. Apart from the difference in age (P.48831 is from Hakel) one feature separates it from *Ichthyotringa furcata* found in the Sahel Alma deposits, this being the forward migration of the mandibular articulation to a point below the orbit. Hay (1903 : 432) erected a new species for a rhinellid from Hajula in the Lebanon on a small specimen mentioned above. The two specimens clearly belong to the same species.

DESCRIPTION. *Neurocranium*. The neurocranium, without the rostral region, is shown in dorsal view in Text-figure 5. The frontals meet in the mid-line in a sinuous suture and form the major part of the skull-roof, which is flat. The frontals attain their greatest width at the hind end of the orbit above the sphenotics. Here they form the anterior half of the roof of the cranial cavity. Above the orbits the lateral expansions of the frontals are distinctly marked off from the medial regions, the demarcation between these two areas is the tube through which the anterior part of the supraorbital sensory canal ran. At first sight these lateral regions of the frontal appear to be elongated supraorbital bones. The frontals are unornamented except for the slightly raised ridges associated with the course of the sensory canal. The lateral and posterior edges of the frontal do not fuse with the neighbouring roofing bones, but overlap them. The tube which contained the supraorbital sensory canal is indicated by pores opening on to the surface at various points. The main supraorbital sensory canal passed anteriorly above the orbit, forming a demarcation between medial and lateral regions of the frontal. Further subsidiary branches of the supraorbital sensory canal are present within the frontal; one branch extends medially and two posteriorly on to the surface of the pterotic. Two further posterior branches passed on to the dorsal surface of the pterotic. The supraorbital canal also appears to have connected with the infraorbital sensory canal within the frontal on the dorsal surface of the sphenotic. The otic branch of the infra-

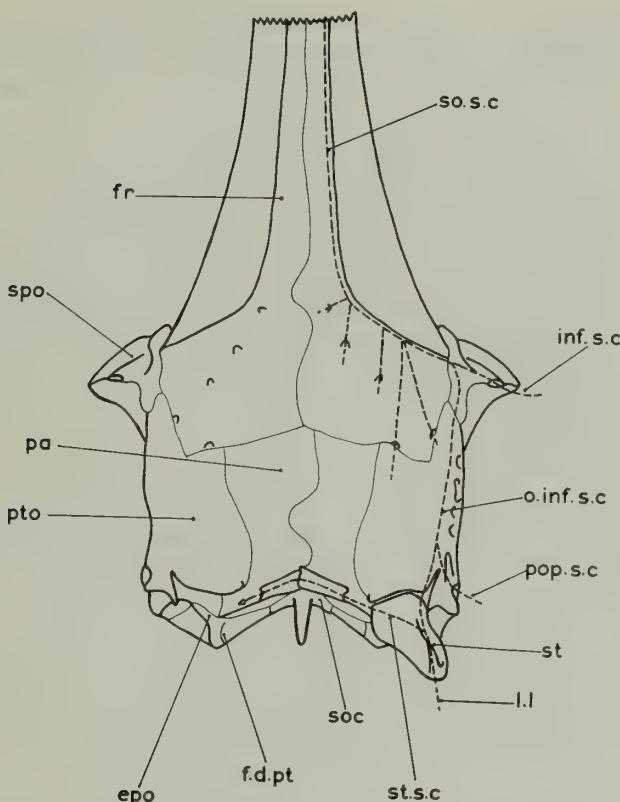


FIG. 5. *Ichthyotringa delicata* (Hay). Neurocranium in dorsal view. The anterior end of the snout is absent and the broken line on the right side of the figure indicates the course of the sensory canals. From B.M.N.H. P.48831.

orbital sensory canal passed forwards within the pterotic to enter the sphenotic. After contacting the supraorbital sensory canal in the frontal the infraorbital canal passed through the sphenotic laterally and down into the last infraorbital bone.

The sphenotic projects laterally from the frontal. The greatest width of the neurocranial roof is between these extremities of the sphenotic extensions. The sphenotic also inclines ventrally. Dorso-laterally the upper surface of the sphenotic is excavated for the reception of the last infraorbital bone.

The pterotic forms the postero-lateral edge of the skull-roof and extends considerably on to the roof. Antero-medially the pterotic is covered by the backward extension of the frontal, but postero-medially it overlaps the lateral edge of the parietal forming the roof of the post-temporal fossa. The pterotic contacts the sphenotic anteriorly and the epiotic posteriorly, the supratemporal lying dorsal to the junction with the epiotic. The dorsal surface of the pterotic is smooth but dorso-laterally several elongated pores open into the tube which housed the otic branch of the infraorbital sensory canal. The most posterior pore is the largest and received the sensory

canal from the preoperculum. The tube in the pterotic opens posteriorly in a shallow groove above the opening of the post-temporal fossa. The posterior end of the fossa is roofed by the supratemporal bone which transmitted the lateral line canal into the rear end of the pterotic.

The parietals are prominent oblong bones meeting in the mid-line in a sinuous suture. Anteriorly the parietals are overlapped by the frontals and laterally by the pterotics. The posterior edges of each parietal are obliquely arranged so that they meet in the mid-line in a shallow V-shaped indentation. Attached to the rear edge of both parietals are small transverse strips of bone each having a grooved dorsal surface. These slips of bone appear to be the remnants of the transverse limbs of the supratemporal. The main part of the supratemporals are small and positioned laterally. The supratemporal sensory canal ran across the skull-roof through both supratemporal bones and across the dorsal surfaces of the parietals and on to these reduced slips of bone.

The supraoccipital is small, just appearing on the roof of the skull. The antero-dorsal extent of the supraoccipital is covered by the parietals. A small supraoccipital crest extends from the posterior face of the bone, but does not rise above the plane of the skull-roof. The supraoccipital contacts the epiotics laterally in a straight suture.

The epiotics extend postero-laterally from the supraoccipital and bear slight dorsal thickenings for the articulation of the dorsal limbs of the post-temporals. The epiotic contacts the parietal anteriorly and forms the postero-medial border to the post-temporal fossa. The dorsal surface of the epiotic and the extreme posterior regions of both the parietal and the pterotic are covered dorsally by the supratemporal.

The parasphenoid is straight and considerably expanded laterally. At the anterior end of the orbit the parasphenoid is an extremely wide flat plate of bone. The lateral ethmoid limits the orbit anteriorly, arising from the ventral surface of the frontal. Ventrally the lateral ethmoid is spread and its medial part appears to attach to the dorsal surface of the parasphenoid. More laterally the lateral ethmoid is free from the parasphenoid and attaches to the postero-dorsal part of the palatine.

In the hind wall of the orbit the pleurosphenoid meets the sphenotic, prootic and the undersurface of the frontal. Joined to the anterior edge of the pleurosphenoid and pressed against the ventral surface of the frontal in the middle of the orbit, is another bone which appears to be the orbitosphenoid. Ventral to the pleurosphenoid a further slip of bone is visible and this may represent the upper end of a basisphenoid.

In front of the orbit overlapping part of the frontal and lateral ethmoid there is a thin, small bone which may represent a nasal or a supraorbital.

REMARKS. The remainder of the description of *Ichthyotringa delicata* will be confined to those features which differ from *Ichthyotringa furcata* or which are exhibited better.

The infraorbital bones, below the orbit, are crushed against the palate but show appreciably better than in *Ichthyotringa furcata*. The two infraorbitals below the

orbit are long and narrow with the second one showing a slight posterior deepening. Three expanded infraorbitals lie posterior to the orbit covering practically the whole of the quadrate, metapterygoid and hyomandibular.

The suspensorium of the lower jaw is inclined forwards with the quadrate condyle situated below the hind end of the orbit, unlike *Ichthyotringa furcata* which has a vertical suspensorium. The hyomandibular curves anteriorly in its lower regions and is shallow. The quadrate is large and forms a continuation of the forward curvature of the lower end of the hyomandibular. The endopterygoid is visible and is connected to the medial region of the ectopterygoid. It is completely covered ventrally with a uniform series of small teeth. The teeth on the ectopterygoid are larger and appear to be slightly recurved.

The preoperculum is considerably larger than in *Ichthyotringa furcata* with the anterior edge curving forwards ventrally following the curvature of the posterior edges of both hyomandibular and quadrate. The posterior edge of the preoperculum remains vertical in position, thus the operculum has an expanded ventral region. The anterior edge is thickened and rounded but more posteriorly it is thinner. The tube which housed the preopercular sensory canal has several openings to the external surface throughout its length. The suboperculum is well exhibited with its anterior edge thickened and extended dorsally as a prominent spine lying medial to the operculum. This antero-dorsal spine is as deep as the main body of the suboperculum itself.

Part of the hyoid arch is visible with a slightly elongated, shallow ceratohyal, followed by a shorter deeper epihyal. A prominent hypohyal lies anterior to the ceratohyal, and a median urohyal extends backwards from the region of conjunction of the hypohyals. At least 8 branchiostegal rays are present (9 appear in *Ichthyotringa furcata*) but there may have been more. The first five articulate with the ceratohyal, the remainder with the epihyal. The branchiostegals gradually increase in thickness from the anterior region but they do not increase in length.

What can be seen of the rest of the body is in agreement with the features already described in *Ichthyotringa furcata*.

Incertae sedis

Genus **APATEODUS** Woodward, 1901

DIAGNOSIS (emended). Head little elongated but large and robust. Post-temporal fossa completely roofed. Parietals only just contact each other in the mid-line. Supraoccipital large. Orbitosphenoid and basisphenoid both present. Jugular canal present in the prootic. Posterior infraorbitals greatly expanded. Maxilla untoothed, forming two-thirds of the gape. Premaxilla laminate and toothed. Large supraorbital bone present. Mesocoracoid arch in the pectoral girdle.

TYPE SPECIES. *Pachyrhizodus glyphodus* Blake.

REMARKS. The genus *Apateodus* is only known by fragmentary material of the head region, thus making it difficult to place with any certainty. Its position close to the genus *Ichthyotringa* will be discussed in the consideration of the suborder Ichthyotringoidei as a whole (pp. 169-176).

***Apateodus striatus* Woodward**

(Text-figs. 6-12)

- 1837 ? *Saurocephalus striatus* Agassiz, 5 : 1 : pl. 25c, figs. 17-20.
- 1844 ? *Saurocephalus striatus* Agassiz, 5 : 1 : 102.
- 1887 *Enchodus corneti* Forir : 37, pl. 1, figs. 2, 3.
- 1901 *Enchodus corneti* Forir ; Woodward : 204 (name only).
- 1901 *Apateodus striatus* Woodward : 260, pl. 13, fig. 6, pl. 14.
- 1902 *Apateodus striatus* Woodward ; Woodward : 38, pl. 11, figs. 1-7, text-fig. 9.
- 1912 *Apateodus striatus* Woodward ; Woodward : 246, pl. 54, fig. 4.
- 1924 *Apateodus corneti* (Forir) ; Kruizinga : 293.
- 1929 *Apateodus corneti* (Forir) ; Leriche : 276.
- 1952 *Apateodus corneti* (Forir) ; Kruizinga : 42.

DIAGNOSIS (emended). *Apateodus* in which the head is large, with a pointed snout. Premaxillae small, toothed and laminate. Maxillae long and rod-like. Maximum depth of the mandible equalling one-fifth of its length. Large teeth on the palatines, ectopterygoid and dentary ; teeth much laterally compressed and marked with fine longitudinal striations.

HOLOTYPE. B.M.N.H. No. 49821, a small skull from the Turonian of Lewes in south-east England.

MATERIAL. The holotype and specimen number 26241 in the Museum of the Institute of Geological Sciences, London: the latter specimen was prepared in acetic acid. This fine head had previously been described and figured by Woodward (1912 : 246, pl. 54, fig. 4). Several specimens were examined in the Musée royal d'Histoire naturelle, Brussels, these being from the Maastrichtian deposits in Belgium and Holland.

DESCRIPTION. *Neurocranium*. The neurocranium is shown in dorsal, ventral, lateral and posterior views in Text-figures 6-9. Posteriorly the neurocranium is broader than it is deep and gradually shallows anteriorly. The front of the neurocranium is acutely pointed, and the orbit occupies the central one-third of its length.

The frontals form the major part of the neurocranial roof, meeting in the mid-line in a sinuous suture. Posteriorly the frontals contact the parietals, also in a sinuous suture. The frontals are flat medially, and relatively unornamented. More laterally they bear several shallow longitudinal ridges which are more concentrated above the region of the supraorbital sensory canal. A shallow ridge passes anteriorly from the centre of ossification above the hind end of the orbit, and demarcates the lateral frontal region. This lateral region is curved to form the upper border of the orbit. The shallow ridge continues anteriorly to form the lateral edge of the neurocranium. The frontal above the orbit is curved, and anteriorly, on a level with the lateral ethmoid, there is a large supraorbital. The supraorbital runs antero-ventrally

continuing the curvature of the frontal around the orbit. A shallow ridge passes postero-medially from the centre of ossification on the frontal and this is continued back on the surface of the parietal. Several small, short ridges extend medially

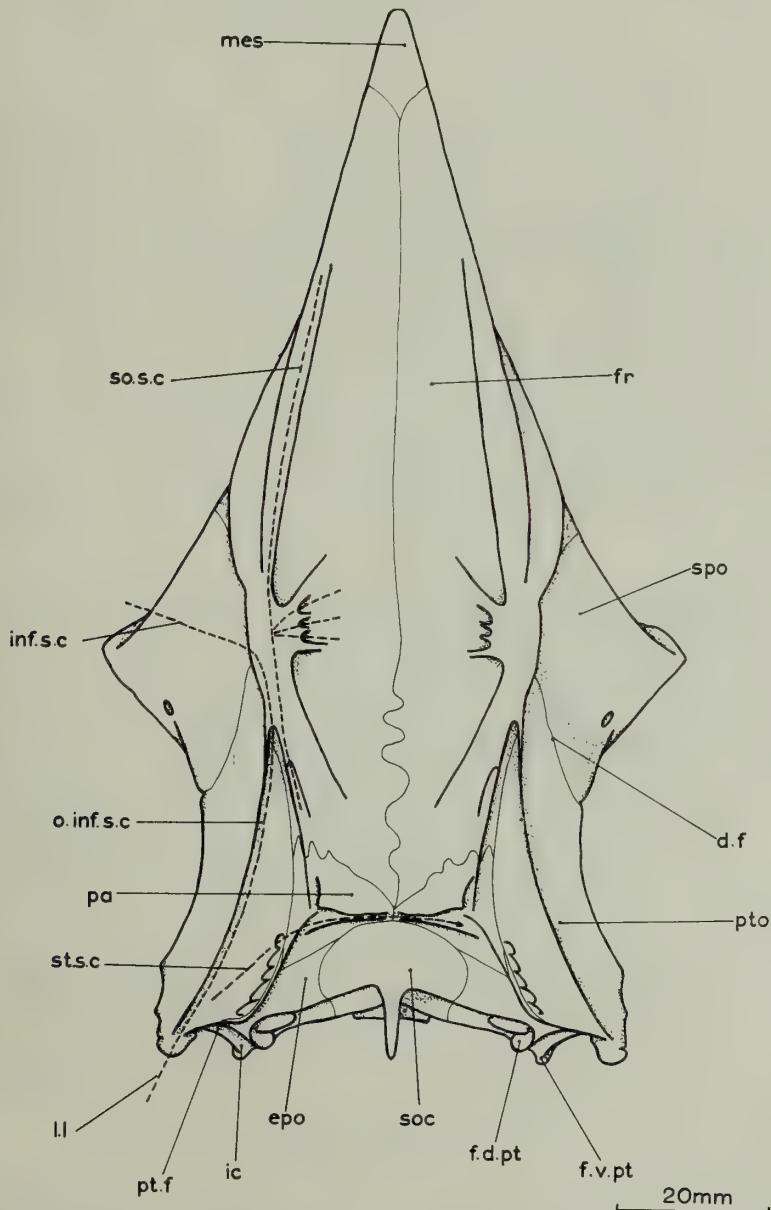


FIG. 6. *Apateodus striatus* Woodward. Neurocranium in dorsal view. The broken line on the left side of the figure indicates the course of the sensory canals. From the collection of the Institute of Geological Sciences, number 26241.

from the centre of ossification. Postero-laterally the frontal meets the sphenotic above the hind end of the orbit and posterior to this is overlapped by the medial extension of the anterior region of the pterotic. The extreme anterior extent of the pterotic roofs the anterior end of the post-temporal fossa, while the frontal also contributes to the antero-medial walls and roof of the fossa. The ventral surface of the frontals bears a broad median channel which is bridged posteriorly by the orbito-sphenoid and the pleurosphenoids.

The parietals are partially separated in the mid-line by the expansion of the supraoccipital, but meet anterior to the supraoccipital in a short suture. Each parietal bears a shallow, transverse crest which contacts its fellow in the mid-line. The lateral extremities of these crests join with the ridges passing back on to the parietals from the frontals. The combined crests so produced pass postero-laterally from the parietals on to the epiotics, terminating on the rear edges of the neurocranium above the post-temporal fossae. Laterally the parietal is overlapped by the medial extension of the pterotic in the roof of the fossa.

The supraoccipital is large and appears on both the posterior and dorsal faces of the skull. Laterally the supraoccipital meets the epiotics on both the dorsal and posterior surfaces of the neurocranium. Ventrally on the posterior face of the skull the supraoccipital contacts the exoccipitals. From the rear face of the supraoccipital a moderately large crest projects posteriorly but does not rise above the plane of the skull-roof.

The epiotics form part of the occipital border, contacting the parietals anteriorly and being overlapped by the medial extension of the pterotic. On the posterior face of the neurocranium the epiotics contact the exoccipitals ventrally. The lateral surface of the epiotic forms the posterior part of the medial wall, roof and floor of the post-temporal fossa. The fossa is complete and opens by a discrete fenestra on the posterior face of the neurocranium. Its roof and medial wall are composed of frontal, parietal and epiotic while the lateral part of the fossa seems to be composed solely of pterotic, but there may possibly be inclusions from the sphenotic and the prootic in the anterior region of the fossa. On the dorsal surface of the epiotic just medial to the post-temporal fossa, the epiotic is thickened into a slight knob which provides the articulatory facet for the dorsal limb of the post-temporal.

The sphenotic contacts the frontal laterally and forms the upper posterior border to the orbit. The dorsal surface of the sphenotic is excavated and smooth and forms the anterior part of the ill-defined dilatator fossa. Near to the lateral edge of the sphenotic a small foramen may have transmitted a branch of the otic nerve.

The pterotic joins the sphenotic anteriorly in the dilatator fossa and extends medially above the post-temporal fossa. The pterotic inclines ventro-laterally, and has a shallow postero-laterally directed crest along its entire length.

The supraorbital sensory canal ran within the frontals anteriorly above the orbit and posteriorly back towards the parietal. Several subsidiary branches of the main canal passed on to the smooth medial region of the frontal and there might have been a complete frontal commissure, as in *Aulopus* (p. 204), and many other myctophiforms (Gosline, Marshall and Mead, 1966 : 7). The lateral line canal entered

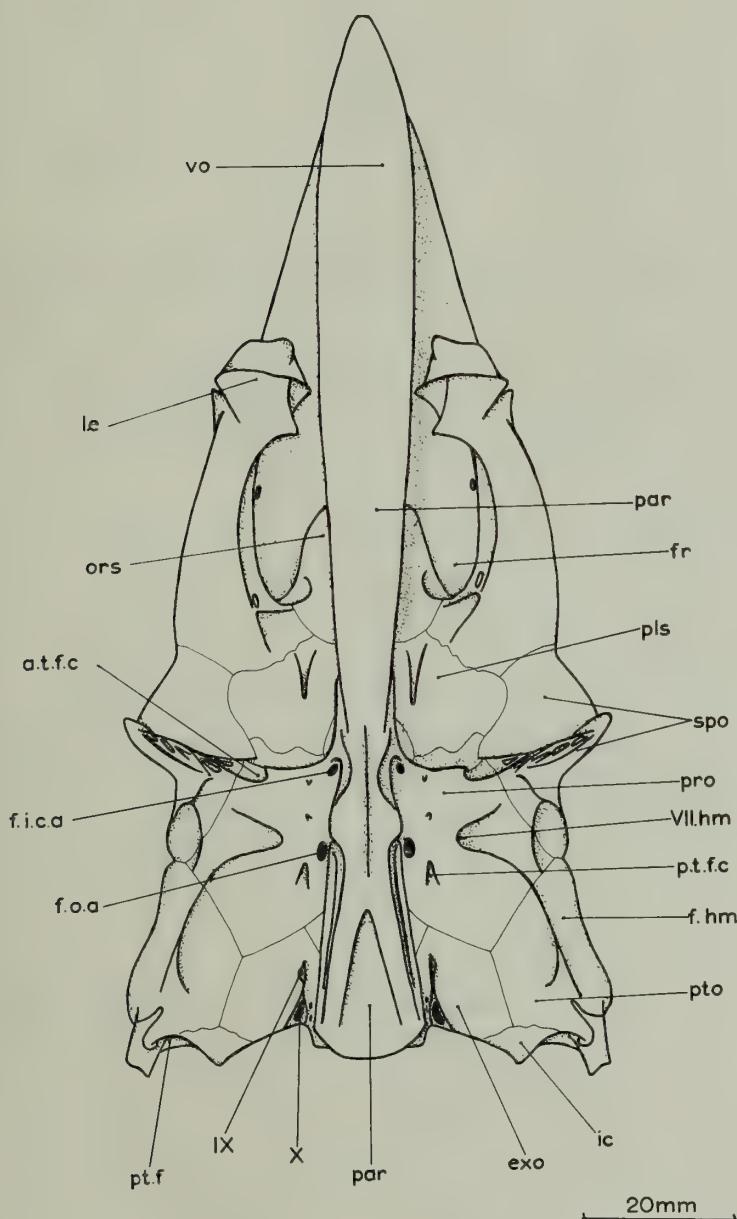


FIG. 7. *Apateodus striatus* Woodward. Neurocranium in ventral view. From the collection of the Institute of Geological Sciences, number 26241.

the posterior end of the pterotic through a small pore and continued anteriorly within the pterotic as the otic branch of the infraorbital sensory canal. The main infraorbital sensory canal traversed the antero-dorsal region of the sphenotic and passed into the frontal, where it contacted the otic branch. The infraorbital canal and the supraorbital sensory canal may have contacted each other within the frontal. A supratemporal sensory canal crossed the roof of the skull on the parietal bones and entered the pterotic laterally above the post-temporal fossa. The pterotic in this region bears several flattened pores through one of which the supratemporal canal appears to have passed. Within the pterotic the supratemporal canal may have joined the otic branch of the infraorbital sensory canal.

The mesethmoid appears to be small, forming the anteriormost region of the snout. The mesethmoid contacts the vomer, and their combined lateral surfaces provide the articulatory region for the internal face of the palatine.

The lateral ethmoids are stout, well ossified bones firmly attached to the underside of the frontals and forming the anterior boundary of the orbit. Ventrally the lateral ethmoid is very irregular in outline, this area being filled with cartilage and providing the posterior suspensorial point for the palatine.

The vomer is an extensive untoothed bone, attached to the mesethmoid anteriorly, and extending back below the parasphenoid as a broad flat plate.

The parasphenoid is long and curved and anteriorly overlies the posterior shaft of the vomer. Below the orbit the dorsal surface of the parasphenoid bears a median longitudinal groove ending at the basisphenoid pedicel. This groove presumably served for the insertion of the ventral edge of a membranous interorbital septum. The ascending processes of the parasphenoid arise just posterior to the basisphenoid pedicel and pass vertically upwards to contact the prootics. The foramen through which the internal carotid artery passed lies at the base of the ascending process. Posteriorly the parasphenoid is reduced in depth and is flattened ventrally, where it contacts the ventro-lateral edges of the basioccipital. The parasphenoid ends below the occipital condyle, and the myodome opens posteriorly below the condyle.

The basioccipital forms the lower half of the occipital condyle and contacts the exoccipitals above. The occipital condyle is practically square in outline with a prominent notochordal pit near to the dorsal edge of the basioccipital. The basioccipital, at its anterior end, contacts the prootic and the ascending process of the parasphenoid. Ventrally the basioccipital is grooved where it forms the roof of the posterior myodome. Just anterior to the condyle on the lateral face of the basioccipital is a group of pits and ridges which may have marked the insertion of a ligament from the supracleithral region of the pectoral girdle but this is by no means certain. Internally the basioccipital forms the posterior parts of the otolith chambers and the posterior part of the myodome roof. The basioccipital above the myodome bears a prominent median longitudinal ridge which partially separates the otolith chambers. The basioccipital is inclined antero-dorsally above the myodome and contacts the posterior edges of the prootics. The otolith chambers are continued as recesses on the medial face of the prootics.

The prootics are large, complex bones containing the trigemino-facialis chamber. Ventrally the prootic consists of a single sheet of bone contacting the ascending process of the parasphenoid. More dorsally it divides into two sheets, the inner one curving medially to meet its partner of the opposite side in the mid-line to form the prootic bridge, while the lateral sheet passes dorso-laterally to contact the sphenotic and the pterotic. The lateral sheet is produced medially above the prootic bridge to form the rear face of the orbit. The otolith chambers are closed anteriorly by the

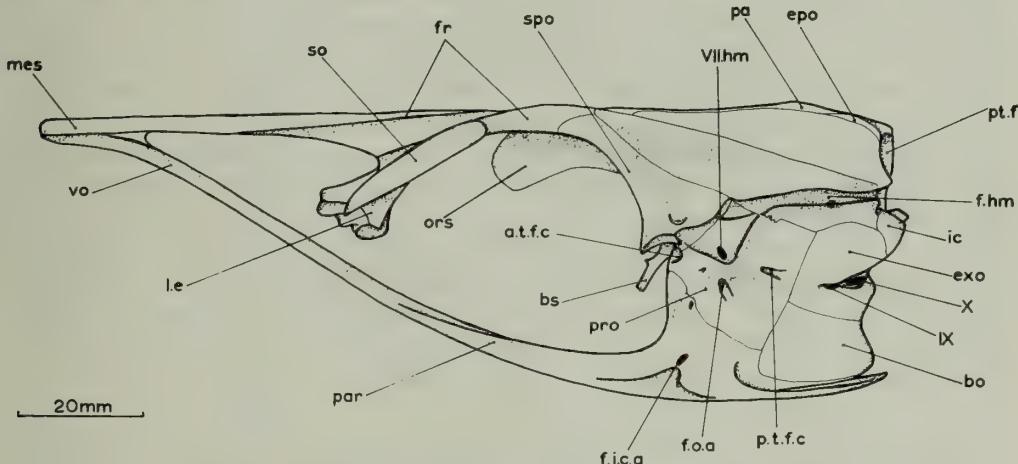


FIG. 8. *Apateodus striatus* Woodward. Neurocranium in lateral view. From the collection of the Institute of Geological Sciences, number 26241.

junction of the prootic bridge with the lateral wall of the prootic. The basioccipital is joined to the hind edge of the prootic bridge and thus separates the cranial cavity from the myodome. At about the middle of its length, the prootic bridge is pierced near its lateral edge, just internal to the anterior extension of the otolith chamber, by a foramen which transmitted the abducens nerve into the myodome. Above the prootic bridge the anterior, orbital face of the prootic is irregular in shape and deeply pitted. This part of the prootic meets the sphenotic dorso-laterally, and the pleuro-sphenoid and basisphenoid medially. The lateral face of the prootic contacts the sphenotic and the pterotic within the hyomandibular facet.

The trigemino-facialis chamber is divided by a bony septum into a medial pars ganglionaris and a lateral pars jugularis. The pars jugularis is a long horizontal canal lying within the prootic, lateral to the pars ganglionaris. The canal opens posteriorly near to the rear edge of the prootic through a small elongated foramen. The canal widens anteriorly and opens into the rear face of the orbit. There are two foramina leading from the pars ganglionaris into the pars jugularis. The more posterior foramen is the facial foramen which transmitted the hyomandibular branch of the facial nerve. The more anterior foramen is the trigeminal and transmitted the trigeminal, buccal, otic, superficial ophthalmic and profundus nerves. The palatine nerve did not enter the pars jugularis but instead passed ventrally

through a small foramen medial to the facial foramen into a canal which opens ventrally into the myodome. The posterior opening of the jugular canal only transmitted the jugular vein. Dorso-lateral to the pars jugularis a large foramen transmitted the hyomandibular nerve. Ventro-laterally a small foramen leads upwards through a canal into the pars jugularis, and this carried the orbital artery. Through the anterior opening of the pars jugularis the jugular vein, the orbital artery, and the buccal branches of both the trigeminal and the facial nerves were transmitted. Two very small foramina are also found in the lateral wall of the pars jugularis and may have transmitted a small artery and vein into the muscle masses next to the prootic. Several additional foramina are found in the hind wall of the orbit. The otic nerves from the anterior opening of the pars jugularis passed upwards into the sphenotic through several elongated foramina. Medial to the anterior opening of the pars jugularis a large foramen transmitted the superficial ophthalmic nerves, the profundus, and probably a mandibular branch of the facial or the trigeminal. The superficial ophthalmic nerves passed dorsally on to the face of the pleurosphenoid where their course is marked by a groove. A further small foramen in the hind wall of the orbit dorso-medial to the other foramina may also have transmitted superficial ophthalmic nerves. The oculomotor passed through a foramen lying ventro-lateral to the suture between the basisphenoid and the prootic.

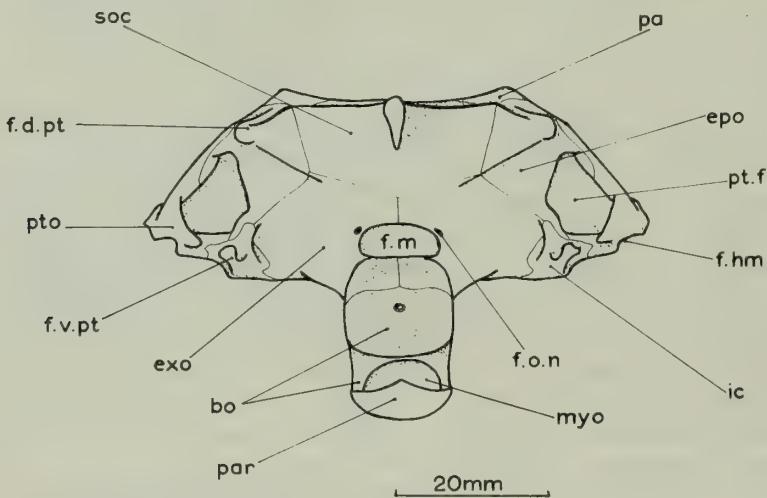


FIG. 9. *Apateodus striatus* Woodward. Neurocranium in posterior view. From the collection of the Institute of Geological Sciences, number 26241.

The exoccipitals meet in the mid-line on the posterior face of the neurocranium and enclose the foramen magnum. Each exoccipital forms part of the occipital condyle together with the basioccipital. The exoccipitals contact the supraoccipital dorsally, the epiotics laterally and the intercalar ventro-laterally. On either side of the foramen magnum are two small foramina which transmitted occipital nerves to the vertebral column. On the lateral face of the skull the exoccipital meets the basioccipital ventrally, the prootic anteriorly, the pterotic dorsally and the intercalar

postero-dorsally. A large foramen in the lateral wall of the exoccipital transmitted the vagus nerve. Anterior to the vagus foramen is a further smaller foramen for the glossopharyngeal nerve.

The pterotic makes up the posterior two-thirds of the hyomandibular facet and contacts the prootic and sphenotic anteriorly within the hyomandibular facet. Below the facet, the pterotic contacts the prootic, exoccipital and intercalar.

The intercalar is small and superficial, lying ventral to the posterior opening of the post-temporal fossa. The ventral surface of the intercalar is flattened, but dorsally provides a concave facet for the articulation of the ventral limb of the post-temporal.

The sphenotic is large and forms the postero-dorsal corner of the orbit. Within the orbit the sphenotic meets the prootic ventrally and the pleurosphenoid medially.

The basisphenoid is Y-shaped with a long pedicel which presumably contacted the parasphenoid ventrally, although not evident in the specimen. The upper arms of the Y are spread out and articulate with the medial edges of the prootic above the prootic bridge. These dorsal arms separate the hypophysial fenestra ventrally from the optic fenestra dorsally. The basisphenoid also articulates dorsally with the medial edges of the pleurosphenoids. The basisphenoid pedicel bisects the opening of the posterior myodome, and gave insertion to the posterior edge of the presumably membranous interorbital septum.

The pleurosphenoids are separated in the mid-line by the optic fenestra, which is closed by the orbitosphenoid antero-dorsally and the basisphenoid postero-ventrally. The pleurosphenoids are attached dorsally to the undersurface of the frontals and in this region are only superficially ossified. Along the ventral surface of the frontals the course of the superficial ophthalmic nerves is indicated by several small foramina through which branches of the nerve passed to the organs of the supraorbital sensory canal.

The orbitosphenoid is a large, median, well ossified bone lying anterior to the pleurosphenoids. It contacts the undersurfaces of the frontals dorsally and the olfactory nerves passed through a median foramen in its anterior edge.

Infraorbital bones. The infraorbital bones are shown in lateral view in Text-figure 11. A low elongated lachrymal lies at the anterior end of the orbit, followed by a second shallow infraorbital. The infraorbitals posterior to the orbit are greatly expanded (see also Woodward, 1912, pl. 54, fig. 4) extending back lateral to the preoperculum.

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 10. The hyomandibular is short, broad and forwardly inclined ventrally, with a single elongated head. The opercular process is prominent and projects posteriorly from the upper part of the rear edge of the hyomandibular. On the lateral face a large crest, originating near the posterior region of the head, passes ventrally along the posterior edge of the bone, where it ends abruptly. The upper anterior edge of the preoperculum rests against the rear edge of this crest. Ventrally the hyomandibular tapers to a stout rod of bone. Anteriorly the hyomandibular is thin and covered laterally by the postero-dorsal part of the metapterygoid. On the medial face there is a large antero-dorsal foramen through which the hyoman-

dibular nerve passed. Within the bone the nerve divided ; the opercular nerve left through a small foramen lateral to the opercular process ; the hyoidean and mandibular nerves left through a large foramen in the angle between the base of the opercular process and the lateral crest. There is a possibility that a second branch of the mandibular nerve passed through a foramen on the lateral face of the hyomandibular near to the ventral extremity.

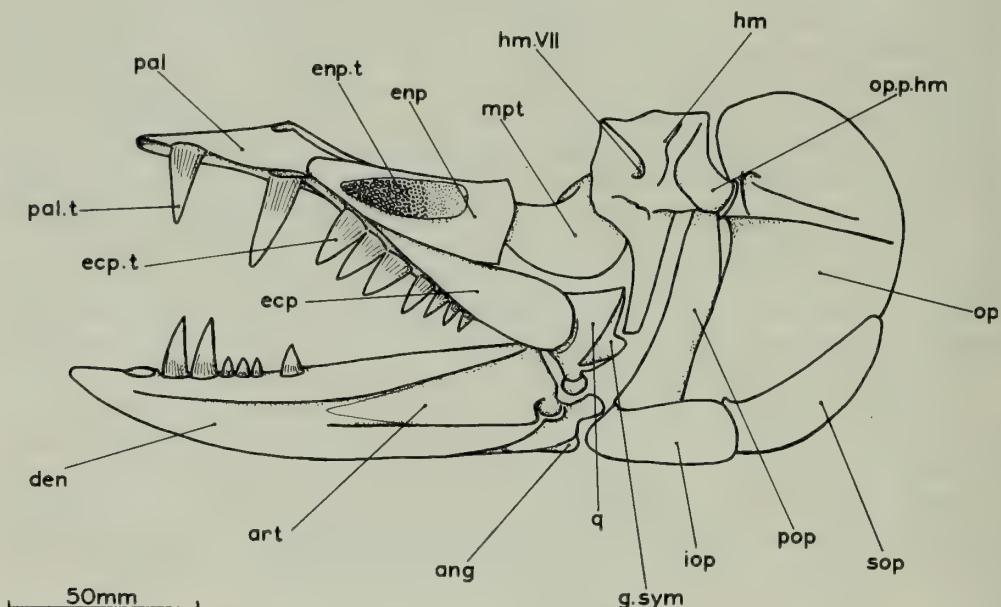


FIG. 10. *Apateodus striatus* Woodward. Hyopalatine and opercular bones and mandible of the right side in medial view. From the collection of the Institute of Geological Sciences, number 26241.

The quadrate is large, triangular and has a prominent transversely arranged, mesially constricted condyle. The groove on the medial face of the quadrate which housed the symplectic is long and shallow and terminates just above the condyle. Posterior to the symplectic groove the postero-dorsal part of the quadrate is emarginated. Anteriorly the quadrate is flattened and extends forwards over the lateral face of the posterior end of the ectopterygoid. On the medial face the ectopterygoid extends back almost as far as the condyle.

The metapterygoid is a thin membranous bone overlying the edges of both the hyomandibular and the endopterygoid but not reaching the dorsal region of the quadrate. Laterally the metapterygoid bears a slight antero-posteriorly orientated crest which forms the leading edge of the metapterygoid ventrally.

The ectopterygoid is laterally compressed posteriorly, but widens anteriorly where it supports teeth. Anteriorly the ectopterygoid joins the palatine, and the medial edge of the ectopterygoid supports the endopterygoid. There are seven large teeth

which decrease in size posteriorly. Each tooth is laterally compressed and acutely pointed with longitudinal striations more noticeable on the unexpanded basal regions (see also Woodward 1912 : 41, fig. 9, and Kruizinga 1924).

The palatine is prominent and overlaps the anterior end of the ectopterygoid both laterally and medially. Both medial and lateral faces of the palatine are flattened and the ventral face of the bone is concave. The ventral concavity supports two prominent teeth, the large one arising at the extreme posterior end of the palatine. The anterior tooth is smaller and much nearer the anterior extremity. The teeth are identical in shape and form to those on the ectopterygoid with which they form a continuous row. The postero-dorsal edge of the palatine is excavated for the reception of the lateral ethmoid. The medial edge of the palatine articulates with the lateral edges of both the mesethmoid and the vomer.

The endopterygoid is thin and inclined dorso-medially. Its ventral surface is convex and bears a large, oval patch of minute teeth.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in the reconstructed skull, Text-figure 11. This is very incompletely preserved. The premaxilla is a small, thin lamina of bone lying alongside the anterior end of the palatine.

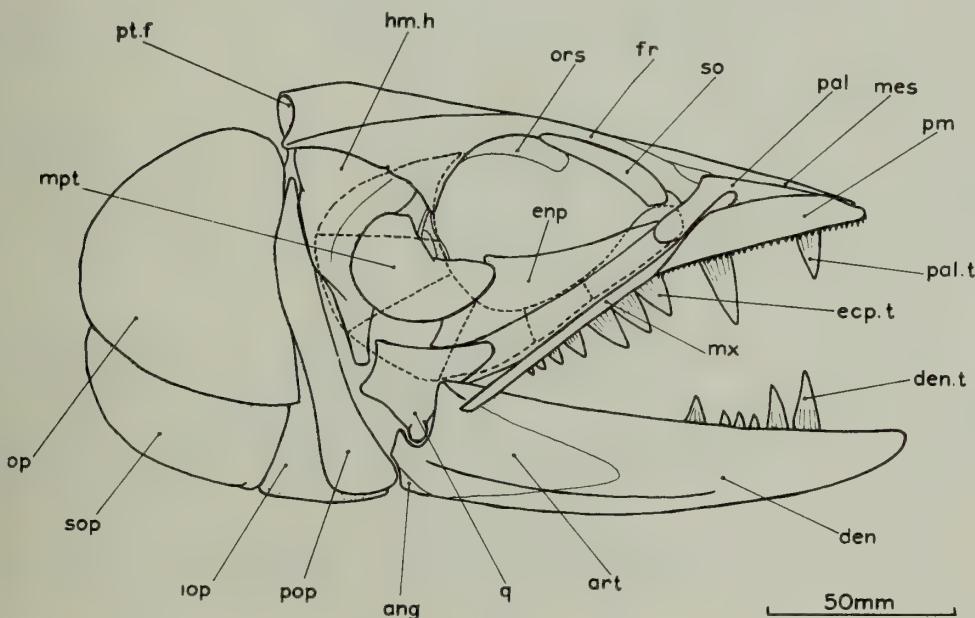


FIG. 11. *Apateodus striatus* Woodward. Restoration of the skull in lateral view.

The upper edge of the premaxilla is rounded but its toothed oral margin is straight. The teeth are minute and the premaxilla extends from the tip of the snout to just behind the level of the lateral ethmoid, thus occupying approximately one-third of the total gape. The maxilla is long, thin and narrow and does not appear to have

borne teeth. Anteriorly the maxilla lies medial to the premaxilla where it is associated with the palatine. Posteriorly the maxilla enters the gape behind the premaxilla. In his original description Woodward (1901 : 260) identified the palatine as the premaxilla and the ectopterygoid as the maxilla. Later Woodward (1912 : 246), using the specimen considered here, identified the bones correctly.

Mandible. The mandible is shown in medial view in Text-figure 10, and lateral view in Text-figure 11. It is long and not particularly deepened. The dentary forms the whole of the oral border of the bone and almost all the ventral border. The posterior edge of the dentary is deeply indented and has a tube opening at the posterior end which is continued as a groove on the face of the articular. This tube and groove housed the mandibular sensory canal. The oral edge of the dentary is thicker and stouter than the remainder of the bone and bears teeth. The teeth are in a single row, of unequal size, and irregular distribution. There are approximately 7 acutely pointed, recurved teeth. The teeth are laterally compressed and arranged at a slightly oblique angle to the long axis of the mandible. The three anterior teeth are the largest and occur a short way back from the symphyseal region. These three large teeth appear to occupy the gap between the two palatine teeth when the jaws are shut. Behind these large teeth, three or four small teeth occur and posterior to these, one or two somewhat larger teeth. The outer face of the dentary is unornamented although several longitudinal ridges are present above the mandibular sensory canal.

The articular facet for the reception of the condyle is concave and transversely orientated. The facet is divided mesially by a ridge of bone corresponding to the mesial constriction of the condyle. The articular has a slight retroarticular process which is laterally grooved for the reception of the mandibular sensory canal.

The angular is a small slip of bone applied to the postero-ventral surface of the articular below the retroarticular process.

Opercular bones. The opercular bones are shown in medial and lateral views in Text-figures 10 and 11. The operculum is large and deep with a concave anterior edge. Posteriorly it is rounded but the ventral edge is obliquely inclined. The outer face of the operculum is smooth and unornamented. The opercular facet is large and in the uppermost region. The facet extends medially and is supported by a strengthening ridge which passes back horizontally across the internal face of the operculum.

The suboperculum is prominent and lies internal to the ventral edge of the operculum. The posterior and ventral edges of the suboperculum are thin and rounded.

The interoperculum is roughly oval in shape with thickened anterior and ventral edges. The interoperculum lies medial to the ventral preopercular region.

The preoperculum is narrow and inclines forwards ventrally. Its anterior edge rests against the posterior face of the hyomandibular crest and the posterior edge of the quadrate. The anterior region of the preoperculum is thickened and contains a deep groove overhung by a flange for the preopercular sensory canal.

Pectoral girdle and fin. The incomplete pectoral girdle is shown in medial view in Text-figure 12. The cleithrum is a large sigmoid bone with a flattened lateral extent and a medially inclined anterior edge.

The scapula is irregularly shaped with a large scapular foramen near its centre. On the posterior edge of the scapula is a large saddle-shaped facet for the articulation of the anterior fin ray. Ventral to this facet the scapula edge is excavated longitudinally forming a facet for the reception of the fin radials.

The coracoid is larger than the scapula and antero-laterally is attached to a medial flange on the internal face of the cleithrum. The coracoid is produced antero-ventrally into a stout flattened process.

A mesocoracoid arch connects the coracoid with the scapula and cleithrum dorsally. The scapula is hollowed out medially to form a well marked canal between it and the mesocoracoid through which passed the dorso-medial muscles of the fin. The mesocoracoid is narrow, with a deep excavation mid-way along its posterior edge.

The pectoral fin consists of at least 15 large, stout rays. Only the proximal parts of the rays are preserved and they are slightly flattened.

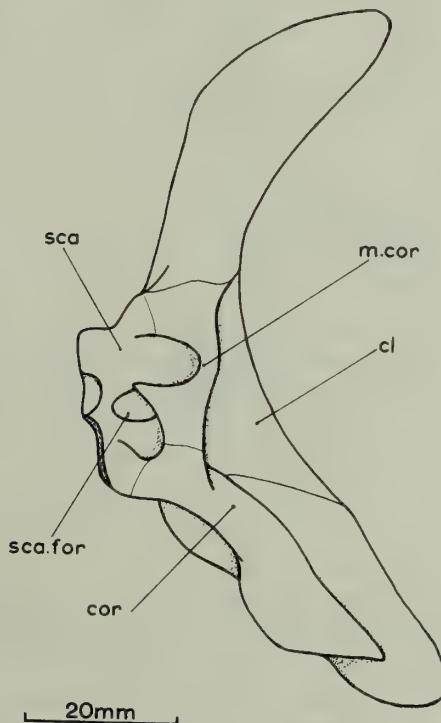


FIG. 12. *Apateodus striatus* Woodward. Part of the pectoral girdle of the left side in medial view. From the collection of the Institute of Geological Sciences, number 26241.

Family APATEOPHOLIDAE nov.

DIAGNOSIS. Head elongated and deepened posteriorly; body deepened but not elongated. Post-temporal fossa unroofed. Parietals separated by the supraoccipital. Orbitosphenoid and basisphenoid absent. Posterior infraorbitals unexpanded. Mandibular suspensorium inclined forwards ventrally. Preoperculum with prominent postero-ventral spine. Vertebral elements incompletely fused; centra as long as deep. Pelvics abdominal, below dorsal fin. Hyomandibular with a double head. Body naked except for scales along the lateral line. Dermal bones ornamented with minute bony tubercles.

Genus **APATEOPHOLIS** Woodward, 1891

DIAGNOSIS (emended). As for the family, only genus.

TYPE SPECIES. *Rhinellus laniatus* Davis.

REMARKS. This species was originally placed in the genus *Rhinellus* by Davis (1887 : 612). Woodward (1888b : 355) later placed the species in the genus *Belonostomus* and later still in the new genus *Apateopholis* (1891 : 634). Ten years later Woodward (1901 : 232) considered *Apateopholis* to be synonymous with *Prionolepis*. In the present work the genus *Apateopholis* is re-erected to contain a single species.

***Apateopholis laniatus* (Davis)**

(Text-figs. 13-15)

- 1887 *Rhinellus laniatus* Davis : 612, pl. 37, fig. 1.
- 1887 *Rhinellus longirostris* Davis : 611, pl. 37, fig. 3.
- 1888b *Belonostomus laniatus* (Davis) Woodward : 355.
- 1891 *Apateopholis laniatus* (Davis) Woodward : 634, pl. 55, fig. 11.
- 1901 *Prionolepis laniatus* (Davis) Woodward : 232.

DIAGNOSIS (emended). *Apateopholis* reaching 10 cm. in standard length. Head with opercular apparatus occupies more than one-third of the standard length. Dorsal fin with 14 rays situated midway along the back. Anal fin with approximately 11 rays, remote in position. Pelvics with 10 rays, opposite the middle of the dorsal fin. Pectoral fins low on the flanks with 16 rays. Lateral line scales not overlapping.

HOLOTYPE. B.M.N.H. specimen number P.4745, from the Middle Cenomanian, Hakel, Lebanon.

MATERIAL. The holotype and specimens in the B.M.N.H., numbers P.4869, P.4026, P.4870, the latter two having been prepared in acetic acid by the transfer method.

REMARKS. The species is only known by these few specimens, but it is difficult to understand why Woodward (1888b, 1901) placed the species in either of the genera *Belonostomus* or *Prionolepis*, since both of these genera possess enlarged shield-like flank scutes. None of the specimens listed above shows any evidence of such enlarged scutes, in fact they are devoid of scales, except along the lateral line. It has

been found convenient to re-erect the genus *Apateopholis* and to ally it with the ichthyotringids, but the differences are such as to warrant its removal into a separate family.

DESCRIPTION. *Neurocranium.* The neurocranium is shown in dorsal view in Text-figure 13. In general shape the neurocranium is long, narrow and deepened posteriorly with a shortened cranial cavity. The anterior region of the neurocranium is drawn out into an extremely long projection which forms the basis of the rostral region. The length of the neurocranium is approximately half that of the body from the occiput to the caudal peduncle. The orbits are enormous, their diameter

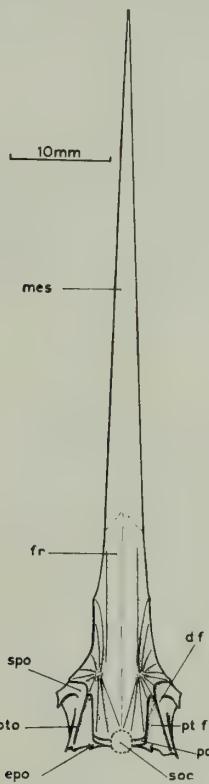


FIG. 13. *Apateopholis laniatus* (Davis). Neurocranium in dorsal view.

being much in excess of the postorbital length of the head. The frontals form the majority of the skull-roof and above the orbit the lateral edge bears an ornamentation of bony tubercles. The sphenotic forms the upper posterior border to the orbit and extends ventro-laterally from beneath the frontal. The sphenotic joins the prootic ventro-laterally to form the anterior part of the hyomandibular facet. The lower edge of the sphenotic and the upper edge of the prootic are both expanded and excavated to produce two cup-shaped depressions into which the anterior region of the head of the hyomandibular rests. Dorsally the sphenotic contacts the pterotic in

a deep depression above the hyomandibular facet; this depression is the dilatator fossa.

The pterotic forms the postero-lateral border of the skull-roof, and bears a high crest which arises antero-medially and terminates at the posterior end of the lateral edge of the bone. This crest forms the boundary between the dilatator fossa laterally and the post-temporal fossa medially. The post-temporal fossa is unroofed. The otic branch of the infraorbital sensory canal passed within the pterotic crest. Above the hyomandibular facet, the postero-lateral part of the pterotic crest bears two large pores. The larger of the two is more ventrally placed and through it passed the preopercular sensory canal; the upper, smaller pore received the lateral-line canal from the post-temporal bone.

The epiotic forms the posterior edge of the lateral region of the skull roof medial to the post-temporal fossa. On the upper region of the epiotic there is a thickened region with which the dorsal limb of the post-temporal articulated. The parietal lies in front of the epiotic and contacts the frontal anteriorly. The post-temporal fossa is composed medially of epiotic, parietal and frontal, and laterally of pterotic. These bones meet in the mid-ventral line of the post-temporal fossa.

The parasphenoid can be seen in the base of the orbit and is expanded laterally into flanges which associate with the endopterygoids. Due to the deepening of the neurocranium posteriorly, the parasphenoid ascends sharply beneath the orbits to pass between the lateral ethmoids.

Jaws and suspensorium. The hyomandibular is long and narrow with a well marked head. Anteriorly the head is expanded and rounded to fit into the cup-shaped depression between the sphenotic and prootic. The posterior part of the hyomandibular head is elongated, narrow and fits into the groove on the pterotic. The axis of the hyomandibular is inclined slightly forwards ventrally, as is the quadrate, thus the mandibular articulation lies below the middle of the orbit. The lateral face of the hyomandibular bears a large crest in its upper region. This crest arises from the anterior region of the head and passes sharply back to the posterior edge of the bone which it follows ventrally. The upper edge of the preoperculum rests against the rear face of this crest. Ventrally the hyomandibular tapers to end some distance above the quadrate. The symplectic is a long ventrally tapering bone contacting the hyomandibular dorsally and the quadrate ventrally.

The metapterygoid overlaps a large part of the lateral face of the hyomandibular, and meets the dorsal edge of the quadrate ventrally. The metapterygoid bears an oblique crest near its anterior border.

The quadrate is irregularly triangular with its posterior edge practically horizontal. The condyle is small and transversely orientated. The posterior edge of the quadrate rests upon the anterior projection of the preoperculum. Both the metapterygoid and the quadrate meet the ectopterygoid anteriorly.

The ectopterygoid runs upwards from the quadrate at an acute angle to contact the palatine below the lateral ethmoids and to support the endopterygoid medially. The palatine is enormously elongated, extending the whole length of the snout region. It is relatively deep posteriorly but shallow anteriorly. The palatine is

supported medially by the mesethmoid and vomer. Both the palatine and the ectopterygoid are furnished with many small conical teeth arranged in a single continuous row.

The exact relationship of the maxilla and premaxilla to one another is uncertain. The premaxilla appears to form practically all of the oral edge of the upper jaw, the maxilla just entering the gape posteriorly. The oral border of both appears to support a continuous row of minute teeth.

The mandible is long, shallow and acutely pointed anteriorly. The oral edge of the dentary bears many small pointed teeth. The articular facet is a shallow semi-circular cavity with no trace of a retroarticular process behind it. Along the ventro-lateral surface of the dentary a deep groove is found which contained the mandibular sensory canal.

The preoperculum is deep and narrow but characteristically expanded ventrally. The anterior edge follows the curved outline of the posterior edge of both hyomandibular and quadrate. The preoperculum ends dorsally just posterior to the upper limit of the crest on the lateral face of the hyomandibular. The near vertical posterior edge of the preoperculum bears a row of prominent tubercles which impart a 'toothed' appearance to the edge. Ventrally the bone is produced into a large

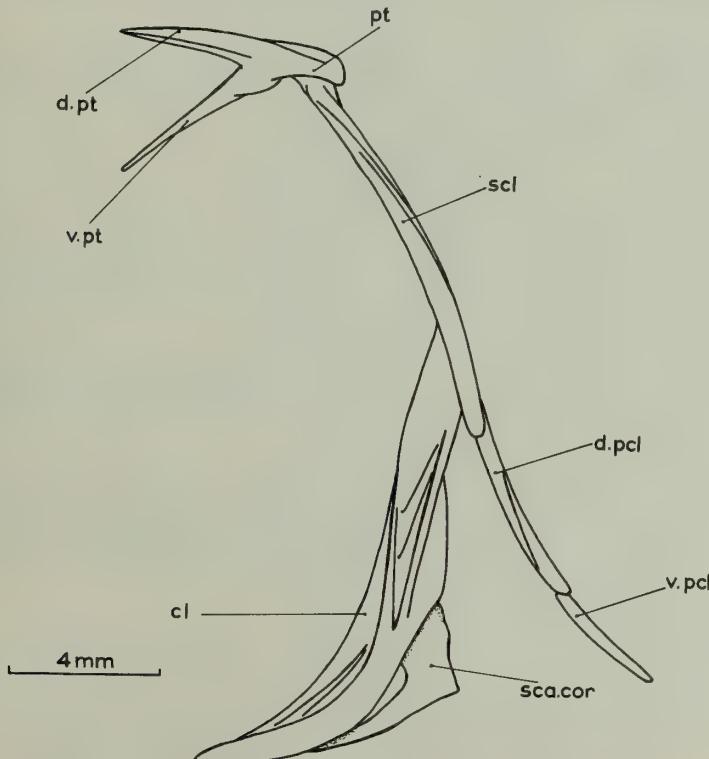


FIG. 14. *Apateopholis laniatus* (Davis). Pectoral girdle of the left side in lateral view.

posteriorly projecting spine. The whole of this expanded ventral part is thickened and ornamented with longitudinal tuberculated ridges. The operculum is deeper than it is broad with the opercular facet contained in the upper half of the anterior edge. The suboperculum is overlapped dorsally by the operculum and is a large bone bearing several strengthening ridges on the lateral face of the anterior region. No trace of an interoperculum was found in the specimens examined.

Pectoral girdle and fin. The pectoral girdle is shown in lateral view in Text-figure 14. The post-temporal has a flattened, slightly arched dorsal limb which is ornamented with longitudinal bony ridges. The long, narrow supracleithrum articulates with the postero-medial region of the post-temporal. The lateral line canal passed through the head of the supracleithrum into the post-temporal. Ventrally the supracleithrum lies against the lateral surface of the uppermost region of the cleithrum.

The cleithrum is large and curved, its anterior edge being inclined medially. The lateral face of the cleithrum is unexpanded and smooth, although bony ridges are present more dorsally. The endoskeletal girdle is attached to the internal face of the cleithrum approximately two-thirds of the way down the bone. The pectoral fin is thus low on the flank and consists of 16 rays, all of which are branched and segmented.

Two postcleithra are also present, both being elongated and narrow. The dorsal postcleithrum arises as a continuation of the supracleithrum posterior to the cleithrum, and the ventral postcleithrum forms a direct continuation of the dorsal one. Both are curved and lie internal to the fin rays.

Median fins and tail. The median fins are shown in the restoration of the complete skeleton in Text-figure 15. The dorsal fin consists of approximately 14 rays and is situated mid-way along the back between the occiput and the base of the caudal fin. The first ray is unbranched, unlike the remainder which are all branched. The proximal radials are elongated and the first few are expanded, particularly the anteriormost which bears an enlarged median keel.

The anal fin is composed of 11 rays and situated behind the level of the rear end of the dorsal fin. The first ray is unbranched as in the dorsal fin, but unlike the dorsal fin none of the proximal radials is expanded.

The skeleton of the caudal fin is impossible to describe with any accuracy. There appear to be either three or four preural vertebrae and two ural vertebrae incorporated into the fin skeleton. The number of principal caudal fin rays is 19 of which 17 are branched. Shorter and unbranched accessory fin rays are present both above and below the caudal fin, approximately 20 in all.

Vertebral column. The entire vertebral column is shown in the restoration of the skeleton in Text-figure 15. It is made up of approximately 43 vertebrae, of which 26 are caudal. The individual centra are about as long as deep and slightly mesially constricted. The neural arches are separate ossifications to the centra, those of the anterior precaudal region being displaced from the centra. More posteriorly the neural arches are more intimately united to the corresponding centra. Prominent

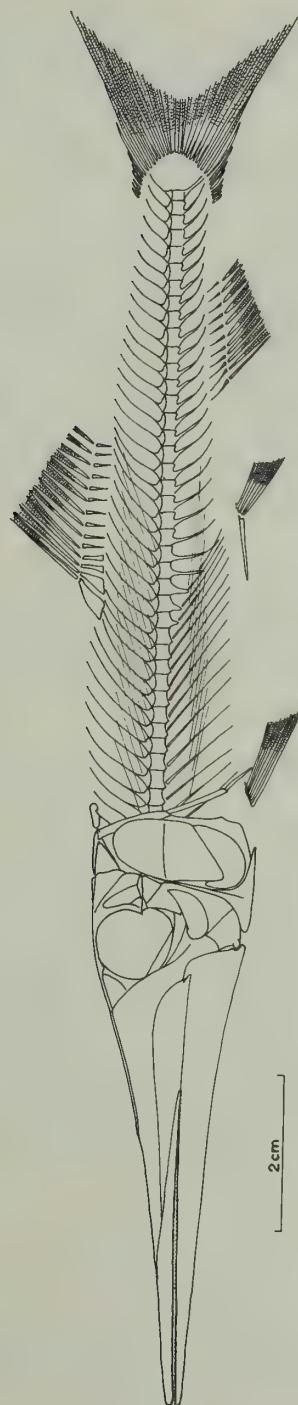


FIG. 15. *Apateopholis laniatus* (Davis). Restoration of the skeleton, scales omitted.

prezygapophyses and postzygapophyses are present on all of the neural arches. Above the anterior region of the vertebral column a noticeably expanded interneural element is present in the dorsal mid-line and appears to be associated with the neural spines of the first two precaudal vertebrae. Prominent antero-ventral transverse processes occur on the precaudal vertebrae with which the pleural ribs articulate. The ribs are long, slender, flattened and tapering. Each rib curves posteriorly and ventrally around the body cavity.

The transverse processes begin to lengthen and extend ventrally at about the 14th precaudal vertebra. The ribs remain in articulation with the haemal arches of the first three or four caudal vertebrae, but these ribs are reduced in length. The haemal spines gradually lengthen on the first few caudal vertebrae. Ventral zygapophyses are present and increase in size in the caudal region.

Intermuscular bones, both epineurals and epipleurals, are associated with the first 25 vertebrae. The epineurals articulate with the neural arches anteriorly, but more posteriorly they shorten and the point of articulation is on the neural spine. Anteriorly the epipleurals attach to the ribs but in the caudal region they are associated with the haemal arches.

Scales. The body is devoid of scales except for a single row along the lateral line. The scales do not overlap, and each is roughly rectangular in shape. The scales bear small posteriorly directed spines on their outer surfaces. On the caudal peduncle at the base of the caudal fin the spines become enormously enlarged and contiguous with one another forming a prominent flange.

Suborder CIMOLICHTHYOIDEI

DIAGNOSIS. Body never deepened but elongated to a greater or lesser extent. Parietals separated by the supraoccipital. Post-temporal fossa either roofed or unroofed, but dilatator fossa always roofed. Orbitosphenoid and basisphenoid absent. Supraorbital occasionally present but no antorbital. Premaxilla prominent, toothed or untoothed but with no ascending process. Maxilla stout, either toothed or untoothed but always entering gape. Teeth present on the vomer and the endopterygoids. Interoperculum absent; branchiostegal rays always numerous. Pelvic fins always abdominal, below dorsal fin. Dorsal fin more or less extended; anal fin always small and remote, near to caudal fin. Vertebral elements incompletely fused, with epineurals and epipleurals in large numbers. Vertebrae variable in number with always less than half being caudal. Fins without spines. Caudal with 19 principal rays. Squamation variable, usually restricted in extent with the predominant scales triradiate.

Family CIMOLICHTHYIDAE nov.

DIAGNOSIS. Body fusiform, relatively shallow and only slightly elongated. Neurocranium shallow, acutely pointed anteriorly and only slightly elongated. Post-temporal fossa incompletely roofed. Jugular canal present in the prootic. Occipital condyle formed only of basioccipital. Maxilla stout and untoothed.

Palatine and ectopterygoid teeth barbed. Small supraorbital bone present and small supramaxilla. 50–60 vertebrae, approximately half being caudal. Ribs borne on small transverse processes. Body bearing two rows of arrow-shaped scutes on each flank.

Genus *CIMOLICHTHYS* Leidy, 1857

DIAGNOSIS (emended). Cimolichthyidae in which the head is somewhat elongated with an acutely pointed anterior region. Palatine with two longitudinal rows of teeth, only innermost row barbed. Ectopterygoid teeth also barbed. Dentary with 3 distinct rows of teeth. Dorsal fin short, mid-way along the back, consisting of 16 rays. Anal fin shorter with 11 rays and remote in position.

TYPE SPECIES. *Cimolichthys levesiensis* Leidy.

REMARKS. The genus was originally erected by Leidy (1857) when he proposed the type species *Cimolichthys levesiensis*, based on palatine and ectopterygoid material showing the characteristic barbed teeth.

Cimolichthys levesiensis Leidy

(Text-figs. 16–21)

- 1835 *Saurodon leanus* Agassiz ; Feuill. : 55 (*errore*).
- 1837 *Saurodon leanus* Agassiz ; 5 ; 1 : pl. 25c, figs. 30, 31 (*errore*).
- 1844 *Saurodon leanus* Agassiz ; 5 ; 1 : 102 (*errore*).
- 1850 *Saurodon leanus* Agassiz ; Dixon : 373, pl. 30, figs. 28, 29 ; pl. 32, fig. 10 (*errore*).
- 1857 *Cimolichthys levesiensis* Leidy : 95.
- 1864 *Plinthophorus robustus* Günther : 115, pl. 6.
- 1878 *Cimolichthys levesiensis* Leidy ; Newton : 790.
- 1878 *Cimolichthys marginatus* (Reuss) Newton : 792.
- 1878 *Cimolichthys lewesiensis* Leidy ; Dixon : 400, pl. 30, figs. 28, 29 ; pl. 32, fig. 10.
- 1888a *Cimolichthys levesiensis* Leidy ; Woodward : 316.
- 1901 *Cimolichthys lewesiensis* Leidy ; Woodward : 221.
- 1901 *Plinthophorus robustus* Günther : 229.
- 1902 *Cimolichthys lewesiensis* Leidy ; Woodward : 44, pl. 9, figs. 10–14 ; pl. 12 ; text-fig. 10.
- 1902 *Plinthophorus robustus* Günther ; Woodward : 48, pl. 12, fig. 5.
- 1902 *Cimolichthys marginatus* (Reuss) ; Leriche : 140, pl. 4, figs. 6–12.
- 1906 *Cimolichthys marginatus* (Reuss) ; Leriche : 96, text-fig. 16.
- 1949 *Cimolichthys marginatus* (Reuss) ; Darteville & Casier : 222.

DIAGNOSIS (emended). *Cimolichthys* in which the maximum width of the neurocranium slightly exceeds one-third of the length. Premaxilla ornamented with radiating tuberculated ridges. Length of mandible five times its greatest depth. Four ectopterygoid teeth, the foremost two being apically barbed. Approximately 60 vertebrae of which 30 are caudal. Centra slightly longer than deep and mesially constricted. Pectoral fin with 12 rays, pelvic fin with 10 or 11 rays arising below the posterior region of the dorsal fin. Dorsal fin with 15 or more rays, anal fin with 10 rays. Body naked except for two rows of imbricate, arrowhead-shaped scutes on each flank.

HOLOTYPE. B.M.N.H. specimen number 4039, an imperfect left ectopterygoid from the Chalk of Sussex.

MATERIAL. Specimens in the B.M.N.H., notably numbers P.1810a and P.1811. The latter specimen was figured by Woodward (1902 : 45, pl. 12, fig. 1), and both specimens were prepared in acetic acid. The holotype of Günther's (1864) *Plinophorus robustus*, number 38113 in the B.M.N.H. (figured by Woodward, 1902, pl. 12), was also examined and is placed in this species as Woodward (1901 : 229) tentatively proposed.

REMARKS. Leidy's naming of *Cimolichthys levesiensis* on palatine and ectopterygoid material was the first recognizable description of the species after Agassiz's errors in ascribing these to the genus *Saurodon*. Between these two references Reuss (1845) had described isolated teeth of a cimolichthyid as the fin spines of a shark. Leriche (1902) synonymized the two species under the name *Cimolichthys marginatus* (Reuss). However Leriche was definitely using *Cimolichthys levesiensis* material, whereas the earlier material used by Reuss was not so definitely attributable to this species.

The following are the references to *Cimolichthys marginatus*

- 1845 *Spinax marginatus* Reuss : 8, pl. 4, figs. 10, 11.
- 1848 *Acanthias marginatus* (Reuss) Giebel : 301.
- 1855 *Anenchelum marginatum* (Reuss) Hébert : 350, pl. 27, fig. 4.
- 1874 *Anenchelum marginatum* (Reuss) ; Barrois : 131.
- 1874 *Trichiurides (Anenchelum) marginatum* (Reuss) Winkler : 39.
- 1875 *Saurocephalus marginatus* (Reuss) Geinitz : 226, pl. 43, fig. 38.
- 1887 *Saurodon marginatus* (Reuss) Dames : 77.
- 1897 *Saurocephalus marginatus* (Reuss) ; Leonhard : 69, pl. 6, fig. 17.

DESCRIPTION. *Neurocranium.* The neurocranium is shown in dorsal, ventral, lateral and posterior views in Text-figures 16 to 19. It is long and shallow with the maximum width occurring behind the orbits. The snout is very acutely pointed but the neurocranium gradually becomes wider more posteriorly.

The frontals form practically the whole of the skull-roof and are long tapering bones ending anteriorly by insertion on to the rear edges of the mesethmoid. Each frontal meets its fellow in the mid-line in a straight suture and overlaps the parietal and supraoccipital posteriorly. Postero-laterally the frontal is excavated above the sphenotic and the pterotic and only enters slightly into the roof of the post-temporal fossa. The surface ornamentation of the frontal is confined to the more lateral regions and is in the form of ridges of bone radiating from the centre of ossification above the sphenotic. The ridges which extend anteriorly terminate on the lateral edge of the frontal anterior to the orbit, those ridges which extend antero-laterally terminate on the edge of the frontal where it forms the upper border of the orbit. The ridges which extend posteriorly are arranged in a fan, each ridge ending on the edge of the frontal where it overlaps the other roofing bones posteriorly.

The supraoccipital extends on to the skull-roof and forms part of the hind wall of the neurocranium. Anteriorly the supraoccipital is overlapped by the frontals and

separates the parietals and the epiotics. The rear face of the supraoccipital gives rise to a small backwardly projecting crest which does not extend above the plane of the skull-roof.

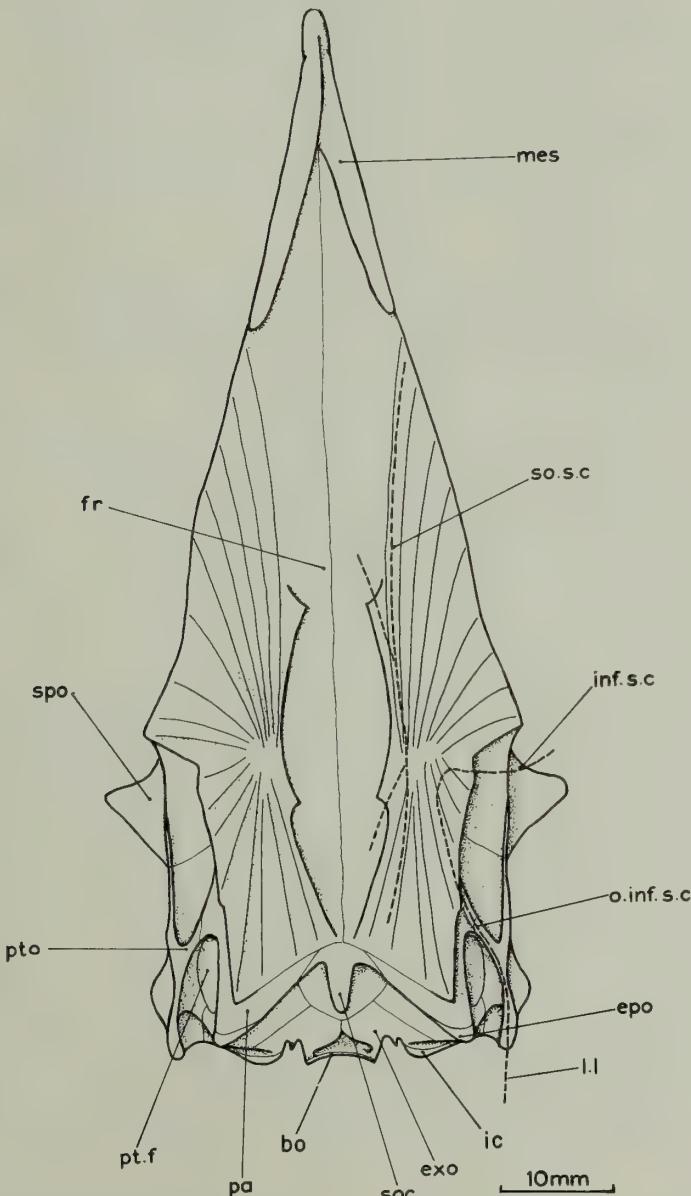


FIG. 16. *Cimolichthys levesiensis* Leidy. Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals. From B.M.N.H. number P.1811.

The parietals are narrow, transversely orientated strips of bone, which laterally form part of the medial wall of the post-temporal fossa, meeting the pterotic anteriorly and the epiotic posteriorly. The post-temporal fossa itself is small and appears to be only partially roofed. Posteriorly where the fossa is unroofed it is bounded medially by the epiotic and the parietal, and laterally by the pterotic.

The epiotics form part of the occipital border of the skull-roof, bounding the parietals posteriorly. On the posterior face of the neurocranium they are separated medially by the supraoccipital, and ventrally contact the exoccipital. Within the posterior region of the post-temporal fossa, the epiotic meets the pterotic in the mid-line of the floor of the fossa. The whole occipital border of the roof is angled sharply backwards from the midpoint on the supraoccipital, the epiotic forming the termination of this backward extent.

The sphenotic extends laterally from beneath the frontal in the posterior orbital region and is smooth and unornamented. A slight crest originates on the sphenotic and extends posteriorly to be continued on the pterotic, the whole extent of this crest forming the postero-lateral border of the skull-roof.

The pterotic forms the postero-lateral part of the roof of the skull and bears two dorsal crests. The lateral crest is the continuation of the crest on the dorsal surface of the sphenotic, whilst the more medial crest originates beneath the lateral edge of the frontal and extends postero-laterally to connect with the lateral crest about midway along the length of the pterotic. This medial crest forms the posterior edge of the incomplete roof to the post-temporal fossa, and the combined crests posteriorly form the lateral boundary of the unroofed portion of the post-temporal fossa.

The supraorbital canal passed forwards within the frontal giving rise to several subsidiary branches which passed on to the surface of the frontal. Two branches passed postero-medially from the region of the centre of ossification, a further branch passed antero-medially and opened on to the interorbital area through a slit-like opening. The main supraorbital canal continued anteriorly within the frontal. The infraorbital sensory canal appears to have passed through part of the dorsal surface of the sphenotic and opened on to the surface medial to the sphenotic crest. The otic branch of the infraorbital sensory canal entered the pterotic crest postero-lateral to the rear end of the post-temporal fossa and passed forwards within the crest. The tube which contained the sensory canal opens anteriorly on the surface of the pterotic in the angle between the two pterotic crests. The contained sensory canal passed forwards on the surface of the pterotic and the sphenotic to connect with the main infraorbital canal on the dorsal surface of the latter bone. A supratemporal commissure does not appear to have been present.

On the edge of the frontal, in the anterior orbital region, a small supraorbital bone is present. The supraorbital bears an external ornamentation of raised ridges of bone radiating ventrally from a point near to the mid-dorsal border.

The mesethmoid is prominent but not heavily ossified. It extends from the anterior end of the frontals and ends in an acute point. Its basic form is that of two laminae of bone fused irregularly in the anterior region and diverging posteriorly to lie alongside the antero-lateral edges of the frontals. The two backwardly divergent

processes are slightly rolled at the edges to give a longitudinally concave dorsal aspect. Woodward (1902 : 45, pl. 12, fig. 1) termed these pieces the nasals, due to their elongated and rolled form. It is quite possible that fusion has occurred and that the nasals have become combined with the mesethmoid, no trace of nasals having been found in the specimen. The lateral edges of the mesethmoid lie along

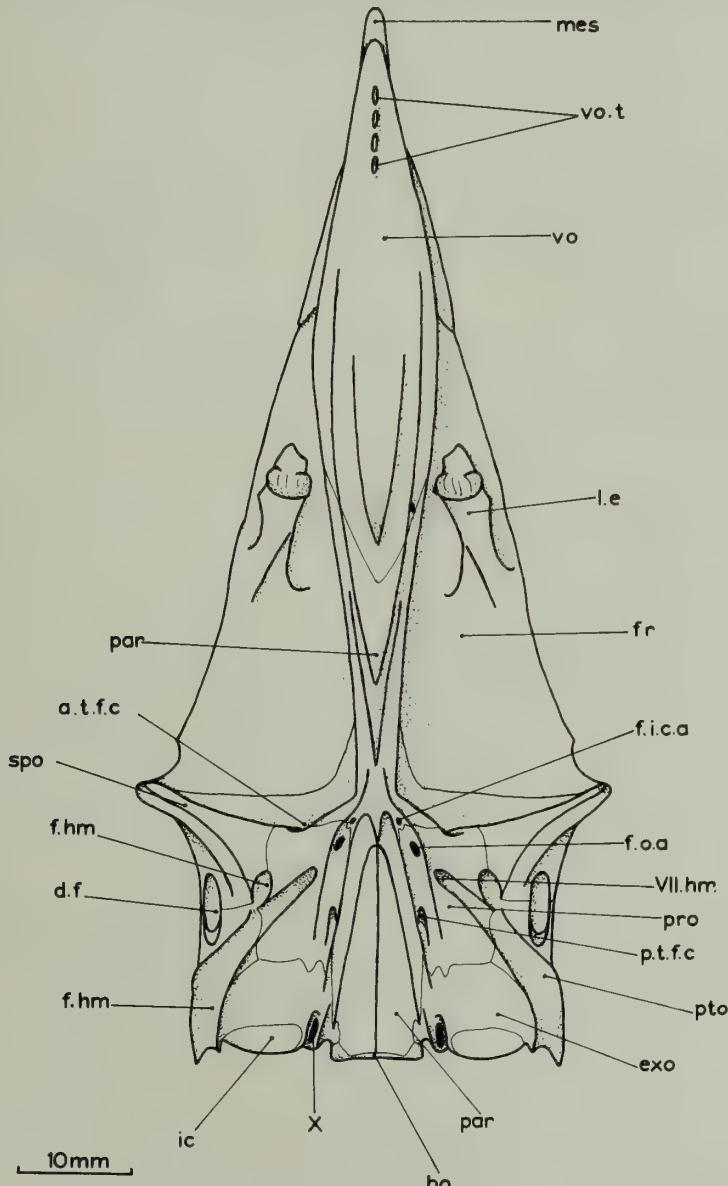


FIG. 17. *Cimolichthys levesiensis* Leidy. Neurocranium in ventral view.
From B.M.N.H. number P.1811.

the dorso-medial regions of each palatine thus providing an articulatory facet for those bones.

The vomer is large and wide although extremely shallow. Anteriorly it tapers to a point and is attached to the underside of the extreme anterior end of the mesethmoid. The vomer widens posteriorly and its edges are in close association with longitudinal ventro-medial facets on the palatines. More posteriorly below the lateral ethmoids the vomer tapers and merges into the parasphenoid. The vomer is

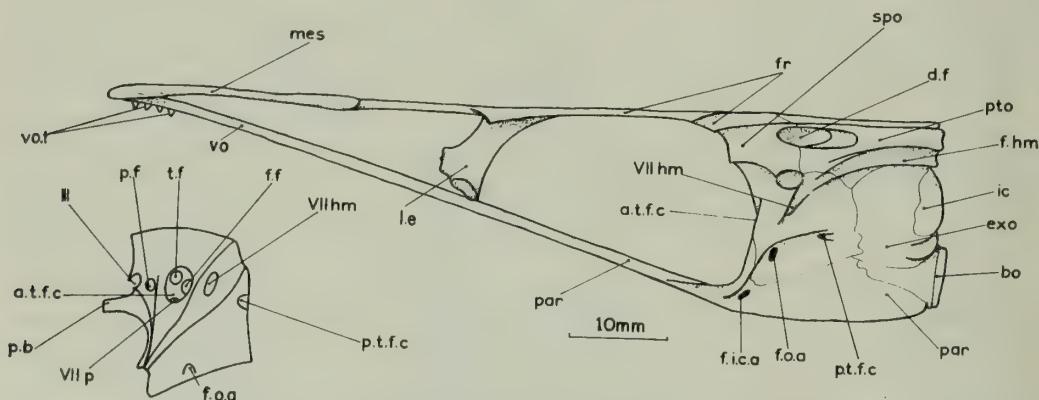


FIG. 18. *Cimolichthys levesiensis* Leidy. Neurocranium in lateral view. The inset shows a diagrammatic representation of the prootic in antero-lateral view. From B.M.N.H. number P.1811.

toothed in its anterior region, and the teeth are in a median row, there being four teeth in all. The bases of the teeth are clearly observable although none of the teeth were present on the specimen examined.

The lateral ethmoids are poorly ossified bones, especially medially. Each is composed of thin sheets of bone which represent superficial ossifications of cartilaginous blocks. Dorsally, each lateral ethmoid is attached to the underside of the frontals, and ventrally the only well ossified part of the bone occurs. This is represented by a small crenulated knob, in life capped by cartilage, which articulates with a definite area at the posterior end of the dorsal region of each palatine.

The parasphenoid is long and bent through a shallow angle at the base of the ascending process. The anterior region of the bone is flattened and expanded where it contacts the vomer. The parasphenoid narrows below the orbit and attains its minimum width at the base of the ascending process. The ascending process passes dorsally and contacts the prootic. The foramen through which the internal carotid artery passed into the base of the orbit lies in the ventral region of the ascending process. Below this foramen on the ventro-lateral surface of the parasphenoid there is a shallow depression with which the pharyngobranchial of the first branchial arch articulated. Posteriorly the parasphenoid just contacts the ventral edge of the exoccipital and attaches to the ventro-lateral edge of the basioccipital. The parasphenoid ends posteriorly below the hind end of the basioccipital leaving a small

fenestra between it and the basioccipital. This fenestra opens into the myodome posteriorly, the parasphenoid forming the entire floor of the posterior myodome.

The basioccipital forms the whole of the occipital condyle. The condyle is circular and concave with a very small notochordal pit in its centre. Anteriorly the basioccipital narrows and its undersurface passes antero-dorsally above the myodome forming part of its roof. As well as the posterior part of the roof of the myodome, the basioccipital also enters into the dorso-lateral parts of the wall of the myodome. On the lateral face of the basioccipital near to the condyle there is a group of pits and ridges. Internally the basioccipital forms the walls of the posterior parts of the otolith chambers, and as the ventral surface of the bone is inclined antero-dorsally above the myodome the otolith chambers become partially separated in the mid-line. The basioccipital contacts the rear edge of the prootic bridge anteriorly, and the otolith chambers extend forwards as narrow recesses within the prootics below the facial foramen.

The prootic is a large and extremely complex bone. Each prootic consists of two vertical sheets of bone joined anteriorly and ventrally. The inner sheet contacts the basioccipital behind, separating the myodome from the otolith chamber, whilst the outer sheet forms the wall of the otolith chamber, meeting the parasphenoid below and the exoccipital posteriorly. Dorsally the inner sheet curves medially meeting its fellow in the mid-line, forming the prootic bridge which separates the myodome from the cranial cavity. The lateral sheet curves dorso-laterally to contact the sphenotic and pterotic in the hyomandibular facet and the exoccipital posteriorly. These two divergent sheets of bone are connected anteriorly by a sheet of bone lying in the postero-lateral face of the orbit. This meets the sphenotic dorso-laterally and the pleurosphenoid dorso-medially, and its medial edge forms the margin of the optic fenestra. The trigemino-facialis chamber, within the prootic, is divided by a bony partition into a medial pars ganglionaris and a lateral pars jugularis. The pars jugularis is a long horizontal canal, widest anteriorly, lying within the prootic lateral to the prootic bridge and in the angle between the dorsal and ventral parts of the lateral face of the bone. Two foramina lead from the cranial cavity into the pars jugularis, the more posterior one being the facial foramen which transmitted the hyomandibular and palatine branches of the facial nerve. The anterior, trigeminal foramen transmitted the trigeminal and the buccal, otic and superficial ophthalmic branches of the facial nerve. The pars jugularis has four external openings. The posterior one is an oval foramen opening on the hind edge of the prootic, and this transmitted the jugular vein. Dorso-laterally, below the anterior region of the hyomandibular facet there is a second large dorso-ventrally elongated foramen which transmitted the hyomandibular branch of the facial nerve outwards from the pars jugularis. Below the jugular canal there is a third foramen which opens into a canal passing up into the floor of the pars jugularis, this canal transmitted the orbital artery into the jugular canal. The fourth foramen is the largest and is the anterior opening of the pars jugularis in the hind wall of the orbit. The trigeminal nerve, the buccal and otic branches of the facial nerve, the superficial ophthalmic components of both nerves, the jugular vein and the orbital artery all passed through this anterior

opening. The otic nerve passed dorso-laterally on to the undersurface of the sphenotic to enter the bone through a small foramen. The superficial ophthalmic nerves passed antero-dorsally within a groove continuous across the face of the pleuro-sphenoid to the ventral surface of the frontal. The profundus nerve does not appear to have entered the pars jugularis, there being a small foramen in the hind wall of the orbit medial to the anterior opening of the pars jugularis which may have transmitted it. The oculomotor nerve passed out of the cranial cavity through the optic fenestra and its passage is marked by a deep notch on the medial edge of the prootic just above the prootic bridge. The palatine nerve, which entered the pars jugularis through the facial foramen, passed out through a canal in the floor of the pars jugularis. This palatine canal is confluent with the canal transmitting the orbital artery up into the pars jugularis. Within the myodome, part of the internal wall of the canal is absent so that the confluence of the two canals is clearly shown with that of the palatine nerve entering the myodome and that of the orbital artery entering from the lateral face of the prootic. Two further very small foramina are found in the lateral wall of the prootic dorsal to the foramen of the orbital artery. One of these opens into the same canal which housed the orbital artery and palatine nerve, and could possibly have transmitted a subsidiary branch of the palatine nerve. More likely, however, the two foramina transmitted a small artery and vein supplying the muscle masses in the area above the prootic. The foramen for the abducens nerve is postero-medial to the facial foramen, and the nerve passed ventrally into the myodome.

The exoccipitals meet in the mid-line of the posterior face of the neurocranium both above and below the wide, shallow foramen magnum, completely enclosing it. It has already been noted that the exoccipitals do not enter into the composition of the occipital condyle but each exoccipital is considerably thickened at the lower corners of the foramen magnum. Several small foramina are found in the exoccipital on either side of the foramen magnum and these probably transmitted occipital nerves to

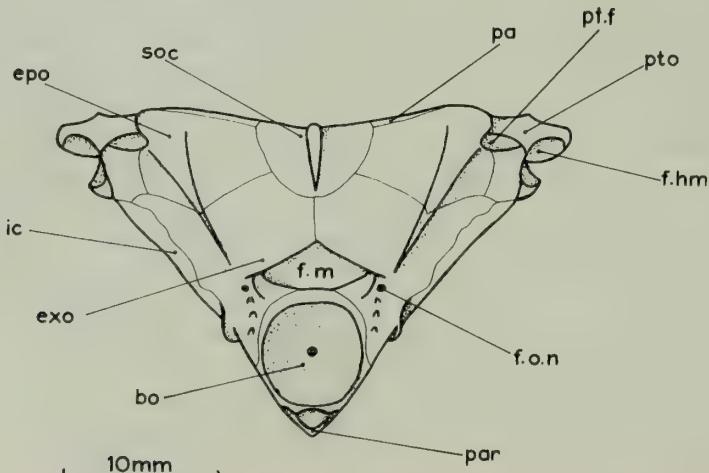


FIG. 19. *Cimolichthys levesiensis* Leidy. Neurocranium in posterior view.
From B.M.N.H. number P.1811.

the vertebral column. A slight dorso-laterally inclined ridge is produced on the exoccipital and is continued upwards by the epiotic as a prominent strut. The exoccipital also appears on the lateral face of the neurocranium since the bone is angled mesially, part lying on the posterior face of the neurocranium and part on the lateral face. The intercalar is attached to the outside of this angle. Laterally the exoccipital contacts the basioccipital ventrally, the prootic anteriorly and the pterotic dorsally. In the postero-ventral angle of the exoccipital the foramen which transmitted the vagus nerve is seen. This foramen is obscured in lateral aspect by a downwardly directed flange of the exoccipital. Slightly anterior to the vagus foramen is the much smaller foramen for the glossopharyngeal nerve.

The intercalar is a small flattened bone on the hind end of the lateral face of the neurocranium, elongated dorso-ventrally and ending below the posterior end of the hyomandibular facet. It does not take part in the composition of the wall of the cranial cavity, being entirely superficial in position and simply providing a point of articulation for the ventral limb of the large post-temporal bone.

The pterotic has already been described in dorsal aspect ; laterally it forms the major part of the hyomandibular facet and is excavated above the facet to produce the posterior region of the dilatator fossa which is a prominent oval fenestra. The pterotic contacts the sphenotic and prootic in the anterior region of the hyomandibular facet.

The sphenotic is large and forms the postero-dorsal corner of the orbital region, the antero-dorsal part of the hyomandibular facet and the anterior half of the dilatator fossa. The hyomandibular facet is shallow posteriorly, anteriorly however it is a well defined cup-shaped facet formed dorsally of sphenotic and ventrally of prootic. Within the orbit the sphenotic contacts the prootic and the pleurosphenoid, and bears a small dorso-laterally directed foramen which transmitted the otic nerve into the sphenotic to innervate the infraorbital sensory canal.

The pleurosphenoids, in the hind wall of the orbit, meet the frontals, sphenotics and prootics. The dorsal region of each pleurosphenoid is only ossified superficially and the more medial regions do not contact the frontal, the contact having been effected through the intervention of cartilage. The groove on the face of the bone, already mentioned in connection with the superficial ophthalmic nerves, passes up towards the ventral surface of the frontal. The course of the nerves along the frontal is indicated by a row of small foramina through which branches of the nerve passed to the supraorbital sensory canal.

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 20. The hyomandibular is short, broad and vertical in position, the quadrate condyle being immediately below the centre of the hyomandibular head. The head region is elongated, and inclined antero-ventrally. The anterior part of the head is thickened and associated with the anterior cup-shaped region of the hyomandibular facet. The remainder of the head is straight and narrow corresponding with the pterotic portion of the facet. The opercular process is not well defined and is merely a thickening of the posterior edge about mid-way down the bone. On the lateral face of the hyomandibular a crest runs postero-ventrally from the anterior region of

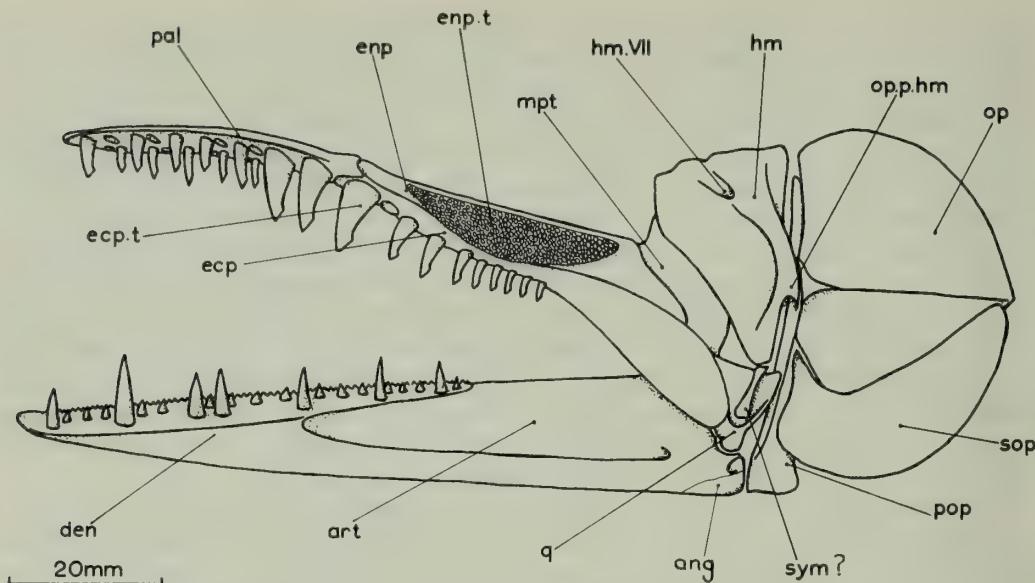


FIG. 20. *Cimolichthys levesiensis* Leidy. Hyopalatine and opercular bones and mandible of the right side in medial view. From B.M.N.H. P.1811.

the head becoming lower and finally terminating near the ventral end of the bone. The preoperculum lies against the posterior face of this crest and is overlapped slightly by it. The hyomandibular tapers ventrally and its anterior extent is thin and covered laterally by the metapterygoid. The hyomandibular branch of the facial nerve entered the bone through a large foramen in the antero-dorsal region of the medial face immediately posterior to the anterior hyomandibular head. The nerve passed within the bone following a course parallel with that of the crest on the lateral face, and divided to give rise to the three main branches of the hyomandibular nerve. The opercular nerve left through a foramen above the opercular condyle in the angle between the main body of the hyomandibular and the lateral crest. The mandibular nerve passed through a foramen below the opercular condyle and here the posterior edge of the hyomandibular is excavated slightly. The mandibular nerve continued ventrally along a groove in the posterior edge of the hyomandibular. The hyoidean nerve may have left in the same region as the mandibular nerve since there is a second smaller foramen below the condyle.

On the internal face of the quadrate a short stout bone is inclined forwards ventrally and is slightly mesially constricted. This bone by its position suggests a symplectic, but in shape it resembles an interhyal.

The quadrate is triangular with a prominent transverse condyle. The groove which housed the symplectic ends ventrally above the condylar region. The posterior edge of the quadrate is slightly thickened and lies against the thickened edge of the lower part of the preoperculum. Anteriorly the quadrate overlaps, laterally, the posterior extent of the ectopterygoid and is firmly attached to it.

The ectopterygoid is bent through a slight angle towards its posterior end where it slopes postero-ventrally to meet the quadrate. Anteriorly the ectopterygoid contacts the postero-ventral region of the palatine and there is a slight angle between the two bones, the palatine not forming a direct continuation of the ectopterygoid. The ectopterygoid bears a single row of teeth ventrally which are not regularly placed. The teeth are firmly fused to the bones and have large expanded bases which are practically circular in cross-section. The teeth themselves become laterally compressed apically to give rise to anterior and posterior cutting edges. The posterior cutting edge is further increased by the production of a post-apical barb. The teeth decrease in size posteriorly. The internal edge of the bone is inclined dorso-medially where it contacts the endopterygoid.

The endopterygoid is a thin sheet of bone lying in a horizontal plane and its internal edge is associated with the lateral edge of the parasphenoid forming the roof of the mouth. Dorsally the endopterygoid is concave where it lies below the orbit. The convex ventral surface is covered by a large, roughly oval patch of minute teeth. Posteriorly the endopterygoid lies medial to the anteriormost extension of the metapterygoid.

The metapterygoid is a thin laminate bone superficially placed so as to cover the posterior extent of the endopterygoid and the anterior expansion of the hyomandibular. Posteriorly the metapterygoid is irregularly rounded but anteriorly there is an oblique ridge forming the upper part of the anterior border; the lower part of the anterior border expands slightly in front of this oblique strengthening ridge. Ventrally the metapterygoid meets the ectopterygoid and the dorsal edge of the quadrate.

The palatine is large and elongated. The ectopterygoid attaches to its ventral surface near the posterior end, which is expanded towards the mid-line, irregularly ridged dorsally and was in life filled by cartilage, providing the articular facet for the ventral region of the lateral ethmoid. The palatine has a convex dorsal surface, but the ventral surface is concave so that an elongated ventral groove is present longitudinally. Anteriorly the palatine tapers to a point and ends on a level with the anterior mesethmoid region. Along the medial face of the palatine two longitudinal grooves are present, a dorso-medial groove along the anterior half of the bone with which the lateral edge of the mesethmoid articulated, and a ventro-medial groove extending practically the whole length of the bone into which the lateral edge of the expanded vomer fits. On the lateral face of the palatine near to the posterior end there is a shallow obliquely orientated groove which houses the anterior end of the maxilla. In the ventral longitudinal groove of the palatine two major tooth rows are found (Woodward, 1902 : 45, fig. 10). The inner row is the more important and is a direct continuation of the row of ectopterygoid teeth. Anteriorly the bone narrows and the teeth are reduced to a single row. At the posterior end of the palatine the teeth become much enlarged and the bone ends with one enormous tooth of the inner row. The teeth are identical to those on the ectopterygoid except that the outer teeth are not provided with a post-apical barb. The inner row of teeth is represented by 11 tooth sockets or teeth and the teeth in the middle of the

row are the smallest. The 11 sockets would presumably indicate the presence of about 5 or 6 functional teeth together with their replacements. The posterior tooth of the palatine and the anteriormost tooth of the ectopterygoid are equal in size and are the largest teeth in the upper jaw. The teeth of the inner row are closely arranged, and their bases are ovoid in shape. The outer row of teeth is of less importance and is represented by smaller unbarbed teeth, which, unlike the inner row, reach their maximum size half way along the bone and decrease in size anteriorly and posteriorly. There are 8 tooth bases present, again probably functional teeth and their successors. Unlike the inner row, the sockets are not quite so crowded together and have a more circular outline. Loomis (1901) has considered the histological structure of the teeth of certain species of this genus from the Niobrara Chalk of the United States.

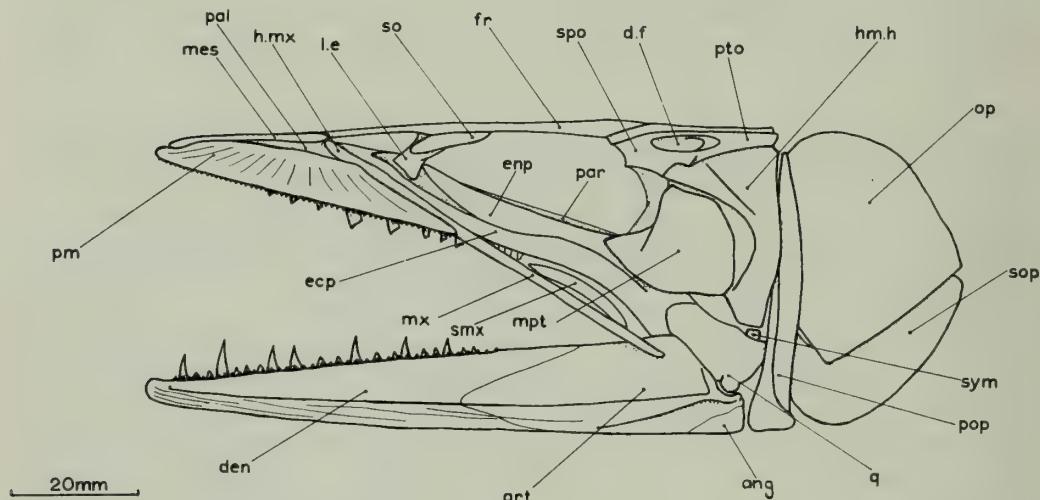


FIG. 21. *Cimolichthys levesiensis* Leidy. Restoration of the skull in lateral view.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 21. The jaw consists of a premaxilla, a maxilla and a small supramaxilla. The premaxilla is a large, antero-posteriorly elongated lamina of bone, tapering at both ends. It is more than four times longer than its maximum depth and its lateral face is ornamented with radiating rows of small bony tubercles. The tubercles radiate ventrally from a point near to the dorsal border of the premaxilla at the region of its maximum depth which is just within the anterior half of the bone. Anteriorly the premaxilla curves around the acutely pointed snout and probably contacted its partner in the mid-line. The oral border of the premaxilla bears a single row of small, conical, closely arranged teeth.

The maxilla is an elongated, stout bar of bone which is straight for most of its length except anteriorly where it is curved medially. The maxilla is smooth, unornamented and bears no traces of having been toothed. The premaxilla forms the anterior half of the oral border of the mouth and the maxilla enters the gape behind it. Anteriorly the maxilla lies in the oblique groove on the lateral face of the palatine, and the curved head of the maxilla is inflected towards the mid-line above the dorso-lateral surface of the palatine. The maxilla was attached to the premaxilla ligamentously.

A small supramaxilla is present on the dorsal edge of the maxilla near to its hind end. The supramaxilla is elongated antero-posteriorly, markedly curved and ornamented slightly with tuberculated ridges.

Mandible. The mandible is shown in medial and lateral views in Text-figures 20 and 21. It is long and relatively shallow, its maximum depth being less than one-fifth of its length, although there is a considerable horizontal extent to the mandible where the ventral edge is curved medially. Anteriorly the mandible tapers to the constricted symphysis. The dentary forms much of the mandible with upper and lower thickened regions joining anteriorly. The thickened dorsal limb bears 3 rows of teeth on its oral side. The extreme oral border bears a close series of minute teeth. Medial to this row there is a second row of larger teeth which are irregularly distributed and unevenly spaced. The internal teeth are the largest and there are approximately 7 in the row. The largest tooth is the second and tooth size decreases posteriorly. The teeth do not bear the post-apical barb so characteristic of the palato-pterygoid teeth, however they are laterally compressed with anterior and posterior cutting edges. All of the teeth in the three rows are conical, hollow, and firmly fused to the jaw by an unexpanded base. The largest teeth are more markedly recurved than the smaller ones.

The articular forms the posterior mandibular region and is inserted on to the internal face of the dentary and occludes the posterior V-shaped indentation of the latter bone. The articular facet is shallow with a mesial ridge corresponding to the constricted condyle. There is no retroarticular process behind the articular facet so that the facet is vaguely defined. Beneath the facet, on the lateral face of the articular, traces of a groove are present in which the mandibular sensory canal ran. The canal was continued in a ventro-lateral groove along the surface of both the articular and the dentary. Ventrally the mandible is considerably thickened and ornamented by prominent longitudinal bony ridges extending forwards from beneath the articular facet, and backwards from the symphysial region on the dentary. The remainder of the lateral face of the mandible is smooth except for the oral border of the dentary where a narrow band of longitudinal ridging is observed.

A minute angular element is visible on the extreme postero-ventral angle of the mandible.

Body. The vertebral column is estimated to consist of approximately 60 vertebrae (50 are shown in B.M.N.H. specimen number 38113). Of these approximately 30–32 are caudal. The precaudal vertebrae bear long narrow ribs supported on small transverse processes. The ribs extend laterally around the abdominal

cavity. All of the vertebrae bear neural arches and spines dorsally, those spines in the precaudal region being long and very slender. In the caudal region the neural spines become shorter and much stouter. The centra are slightly longer than deep and are mesially constricted. Each centrum is strengthened by one or two lateral longitudinal ridges. Epineurals and epipleurals occur on the precaudal vertebrae. The pectoral fins are low down on the flanks and each fin appears to consist of approximately 12 rays. The rays are stout and well ossified with the first ray unbranched. The pelvic fins are abdominal, situated below the mid-point of the dorsal fin. Each pelvic fin consists of 10 or 11 rays. The pelvic bones are large triangular plates meeting in the mid-line of the ventral body wall. The pelvic fins are almost as large as the pectoral fins. The dorsal fin lies within the anterior half of the trunk and is relatively short based. It is composed of approximately 15 rays, but more may have been present. The anal fin is only shown by a few imperfect fragments, and all that can be said is that possibly as many as 10 rays were present; it is remote in position, quite close to the caudal fin. The caudal fin is not represented but part of the caudal skeleton can be seen. The preural vertebrae are about four in number and the centra are reduced in length. The neural and haemal spines are enlarged and somewhat flattened. The first preural vertebra is fused with the first ural vertebra, and the compound centrum so produced supports the parhypural (the haemal spine of the first preural vertebra) and the first two hypurals. These hypurals are fused into a single compound element.

Scales. The trunk is devoid of normal squamation but bears two rows of scutes on each flank, one placed dorso-laterally, the other ventro-laterally. The scutes (Woodward 1902, pl. 12, fig. 5) are overlapping and 'arrowhead' shaped, those in the anterior region of the dorso-lateral row being the largest. Each scute bears a longitudinal raised keel, and the posterior region is broader and slightly corrugated. The scales are longer than they are broad with the anterior region narrow, smooth and slightly lengthened. At the base of the pelvic fin, one of the scutes in the ventro-lateral row has its lower margin excavated to allow for the fin insertion.

Family DERCETIDAE Pictet, 1850

DIAGNOSIS (emended). Body elongated and very shallow; head elongated to a greater or lesser extent. Post-temporal fossa never completely roofed. Maxilla enters gape and supports a single tooth row. Supraorbital and supramaxilla absent. Vertebrae 60–80 in number of which approximately 30 are caudal. Anterior precaudal vertebrae often elongated. Ribs borne on prominent laminar transverse processes. Neural and haemal spines always short. Intermuscular bones extremely abundant. Scales normally confined to one or more continuous rows of enlarged triradiate scutes along the flank, occasionally the remainder of the body covered by much smaller scales.

Genus ***DERCETIS*** Agassiz, 1834

1863 *Leptotrachelus* von der Marck: 59.

1940 *Benthesikyme* White and Moy-Thomas: 102.

DIAGNOSIS (emended). Dercetidae in which the head is more or less extended, with premaxilla produced slightly in advance of the mesethmoid. Body region always extended. Mandible extends to the anterior tip of the snout. Teeth clustered and in the form of slender hollow cones, present on premaxillae, maxillae, dentaries, palatines and ectopterygoids. Paired fins prominent with pectorals larger than the pelvics. Dorsal fin more or less extended, in the mid-region of the back. Anal fin short and remote. A single pair of transverse processes per centrum. Anterior precaudal centra at least twice as long as deep. Dermal scutes in a paired series along dorsal and ventral borders and in a single series along lateral line; a few large lath-shaped intermediate scutes in larger species, but squamation never complete.

TYPE SPECIES. *Dercetis scutatus* Agassiz.

REMARKS. The genus was erected by Agassiz (1834: 390, and Feuill.; 20) to include the type species *Dercetis scutatus* from the Upper Senonian deposits of Baumberg, Westphalia. Later von der Marck (1863) erected another genus within the family Dercetidae to include the new species *Leptotrachelus armatus* (59, pl. 10, fig. 3). In 1873, von der Marck added a further species, *Leptotrachelus sagittatus* (63, pl. 2, fig. 1). Both of these species were erected on imperfect material from the Upper Senonian (Campanian) of Sendenhorst, Westphalia, and his type material is located in the Paläontologisches Institut der Westfälische Wilhelms-Universität, Münster. Since 1873 several more species of both genera, *Dercetis* and *Leptotrachelus*, have been erected, the material coming from various localities such as the Chalk of S.E. England, the Niobrara Chalk of Kansas and from the Sahel Alma locality in the Lebanon.

The holotype of *Dercetis scutatus* (at one time in the Bayerische Staatssammlung für Paläontologie, Munich) appears to have been either lost or destroyed. Unfortunately no other specimens of the type species could be traced. After examination of most of the species placed in the genus *Dercetis* from the English Chalk, together with the examination of both the *Leptotrachelus* species erected by von der Marck, and those leptotrachelids from the Lebanon, it is clear that they all belong in a single genus. This conclusion is in accordance with that of Siegfried (1966: 215), who has examined and redescribed von der Marck's material, and as a result moved both to the genus *Dercetis* (*Dercetis armatus* (Text-fig. 24) and *Dercetis sagittatus*).

Several species of *Leptotrachelus* from Sahel Alma have been studied but all of the material is fragmentary and badly preserved. The descriptions are therefore incomplete but even so are sufficient to show that these species also belong to the genus *Dercetis*. The three species from Sahel Alma, *Dercetis triqueter* (Text-fig. 23), *Dercetis gracilis* (Text-fig. 25) and *Dercetis rostralis* (Text-fig. 26), although still considered to be three separate species, are arbitrarily separated. Thus considering all the *Dercetis* material available a graded series is apparent, ranging from the

largest *Dercetis* species, *Dercetis maximus* from the English Chalk (Woodward, 1903, pl. 15, fig. 2), to the smallest *Dercetis gracilis* from the Lebanese chalk.

White and Moy-Thomas (1940 : 102) pointed out that the generic name *Leptotrachelus* was preoccupied and erected a new generic name, *Benthosikyme*. Since all of the species of *Leptotrachelus* are now included in the genus *Dercetis*, *Benthosikyme* is treated as a synonym.

Dercetis triqueter Pictet

(Text-figs. 22, 23)

- 1850 *Dercetis triqueter* Pictet : 47, pl. 9, figs. 5, 6.
- 1850 *Dercetis linguifer* Pictet : 47, pl. 9, figs. 7, 8.
- 1866 *Leptotrachelus triqueter* (Pictet) Pictet & Humbert : 95, pl. 14, figs. 1, 2.
- 1887 *Leptotrachelus triqueter* (Pictet) ; Davis : 620, pl. 38, fig. 1.
- 1898 *Leptotrachelus triqueter* (Pictet) ; Woodward : pl. 10.
- 1901 *Leptotrachelus triqueter* (Pictet) ; Woodward : 174.
- 1903 *Leptotrachelus triqueter* (Pictet) ; Woodward : 68, text-figs. 15, 16.
- 1926 *Leptotrachelus triqueter* (Pictet) ; Woodward : fig. 3.
- 1940 *Leptotrachelus triqueter* (Pictet) ; Berg : fig. 215.
- 1954 *Leptotrachelus triqueter* (Pictet) ; Signeux : 642, pl. fig. 4.
- 1958 *Leptotrachelus triqueter* (Pictet) ; Bertin & Arambourg : fig. 1617A.
- 1964 *Benthosikyme triqueter* (Pictet) Danil'chenko : fig. 141.
- 1966 *Leptotrachelus triqueter* (Pictet) ; Lehman : fig. 200.

DIAGNOSIS (emended). *Dercetis* of standard length up to 22.5 cm. Vertebrae between 70 and 73 in number of which 30 are caudal. Anterior precaudal centra twice as long as deep. Head equal to approximately one-fifth of the standard length and the maximum height of the head equal to one-third of its length. Preorbital region forms 60% of the total head length. Mesethmoid bluntly bifurcate anteriorly. Dorsal fin with 35 rays; anal fin with 8 or 9 small feeble rays, remote in position. Pectoral fin with 11 rays; pelvic with 8 rays arising behind anterior third of the trunk. Scutes of varying sizes, with the precaudal ones heart-shaped; triradiate pattern obscured in many. Intermediate lath-shaped scutes often present.

HOLOTYPE. Fragment of abdominal region in the Muséum d'Histoire Naturelle, Geneva, from the Upper Senonian of Sahel Alma, Lebanon.

MATERIAL. Specimens in the B.M.N.H., the Muséum d'Histoire Naturelle in Geneva, and the Muséum National d'Histoire Naturelle, Paris.

REMARKS. The species was originally erected by Pictet as *Dercetis triqueter* and in the same work (Pictet, 1850) he erected a second species, *D. linguifer*. Pictet and Humbert (1866 : 95) synonymised both species under *Leptotrachelus triqueter*. Both holotypes (*Dercetis triqueter* and *Dercetis linguifer*) are in Geneva. That of *Dercetis linguifer* is also a small fragment of an abdominal region and is clearly referable to *Dercetis triqueter*.

DESCRIPTION. *Neurocranium.* The neurocranium is indistinct and badly preserved in all of the specimens examined. The neurocranium is elongated,

shallow and widest at the hind end of the orbits. The frontals make up practically all of the skull-roof reaching back almost to the occipital border. Anteriorly the frontals taper to contact the rear edge of the mesethmoid near to the front end of the snout. The frontals widen to form the upper margin of the orbits. Posteriorly the frontals contact the supraoccipital and the parietals. The ornamentation on the frontals radiates in all directions from the centre of ossification above the rear end of the orbit. Rows of minute tubercles pass anteriorly and antero-laterally above the orbit, and posteriorly and postero-medially above the cranial cavity itself. Towards the lateral edge of the frontal above the orbit the ornamentation is no longer in uniform rows but is randomly scattered. The supraoccipital is small, meeting the frontals anteriorly and forming the centre of the occipital border of the skull-roof. The parietals lie lateral to the supraoccipital and are small transversely orientated bones ornamented with tubercles. The pterotic forms the postero-lateral border of the skull-roof, and the rows of tubercles on its dorsal surface originate near the hind end of the bone. The sphenotic projects laterally from beneath the frontal at the rear end of the orbit, but its dorsal surface appears to have been unornamented.

The mesethmoid is in the form of two strips of bone joined anteriorly. These strips flank the extreme anterior ends of the frontals. The mesethmoid is slightly expanded anteriorly into two small lateral wings and bears a median, anterior, U-shaped indentation which imparts a slight bifid appearance. The vomer corresponds to the mesethmoid anteriorly in the possession of lateral wings. The wings are flattened and lie in a horizontal plane and fit into antero-posteriorly elongated facets on the antero-medial faces of the palatine. The vomer only meets the mesethmoid in this anterior region, widening behind to pass back as a prominent flattened plate which attaches to the parasphenoid. Teeth do not appear to have been present on the vomer. The parasphenoid is a straight rod of bone running through the base of the orbit, apparently without lateral flanges.

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 22. The jaws are elongate and bear a prominent armature of long teeth. The palatine bone is long and narrow, and in the form of a curved, thickened lamina with a longitudinal ventral concavity housing the teeth. In the extreme anterior region the bone narrows and the concavity is lost. The medial face of the palatine is excavated producing a facet for the reception of the lateral wing of the mesethmoid. Anteriorly the palatine ends in advance of the mesethmoid, and posteriorly below the anterior region of the orbit. The lateral ethmoid is not prominent and ventrally is weakly associated with the posterior end of the palatine. The teeth are closely packed and give the appearance of having been arranged in three major rows. The teeth are all of the same type, there being minor variations in length and breadth, but all are needle-like with unexpanded basal regions. The diameter of the tooth bases varies little between the large teeth and the small teeth, the major change in dimension is in the length. All of the teeth are hollow and oval in cross-section. The cutting edge of each tooth is confined to the extreme apex where the hollow cavity is occluded and the cross-section of the tooth becomes more elliptical.

The cutting edge extends around the apex imparting a slight barbed appearance to the tooth both pre-apically and post-apically. The teeth are practically straight and most of them are inclined slightly anteriorly rather than vertically downwards. The teeth are shortest at the anterior end and increase in size posteriorly reaching their maximum length about two-thirds of the way back, after which they again decrease in size. The palatine contacts the ectopterygoid below the front end of the orbit and it appears that one of the rows, the most internal, of the palatine teeth

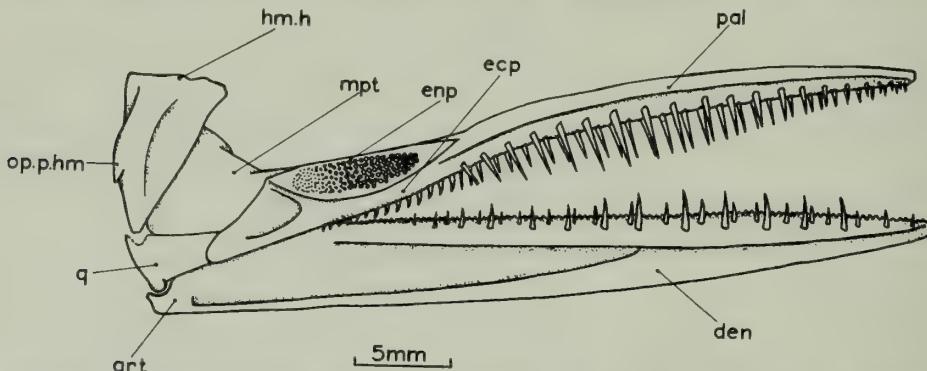


FIG. 22. *Dercetis triqueter* Pictet. Hyopalatine bones and mandible of the left side in medial view.

is continued back on the ectopterygoid. The teeth on the ectopterygoid are, however, shorter, stouter and markedly recurved. Each tooth still exhibits the apical cutting region both in front of and behind the apex. The ectopterygoid is small in comparison to the palatine and inclined at a greater angle to the horizontal. Posteriorly the ectopterygoid meets the quadrate and overlies it laterally. The endopterygoid attaches to the internal region of the ectopterygoid and is in the form of a flat plate lying medially in the roof of the mouth. The posterior region of the ectopterygoid is thickened in two places, the thickenings diverging posteriorly. The lower thickened region contacts the quadrate, the upper thickened region passes postero-dorsally and forms the attachment region for the rear edge of the endopterygoid. This latter thickening is continued postero-dorsally by a thickened crest on the anterior region of the metapterygoid. This bifurcation of the thickened edges of the ectopterygoid is clearly visible from the medial aspect. The metapterygoid is large with an obliquely inclined crest, the remainder of the bone overlying the lateral face of the anterior region of the hyomandibular and attaching to the dorsal edge of the quadrate. The hyomandibular is upright with an elongated head and a shallow lateral crest passing down the rear edge of the bone. The quadrate condyle lies below the level of the occipital border of the neurocranium.

Dermal upper jaw. Due to the fragmentary nature of the specimens it is impossible to ascertain to what extent, if any, the maxilla enters the oral border of the upper jaw. Both premaxilla and maxilla are elongated and lie against the lateral face of the palato-pterygoid. Anteriorly the premaxilla is wrapped around

the end of the palatine. Thus medial to the anterior end of the palatine the premaxilla extends backwards and appears to be associated with the anterior edge of the mesethmoid within the U-shaped indentation of the latter bone. The premaxilla extends posteriorly as a shallow lamina of bone bearing a single marginal row of teeth on its ventral edge. The teeth are small but recurved and have the same apical specialization as the palatine and ectopterygoid teeth. The maxilla appears to have entered the gape posteriorly and borne teeth along its ventral edge.

Mandible. The mandible is shown in medial view in Text-figure 22. The mandible is long and shallow, although it has a considerable ventral extent lying in a horizontal plane. Anteriorly the mandible is acutely pointed and the symphysis is constricted. The dentary is the major component of the lower jaw forming the entire oral border as well as most of the lateral face of the mandible. Teeth are borne on the oral edge of the dentary and are numerous and clustered. All of the teeth are long and needle-like and similar to those on the ectopterygoid in being recurved. The articular facet is ill-defined, being somewhat less than a semicircle and with no retroarticular process posteriorly. The outer face of the mandible is smooth and bears no traces of ornamentation.

Vertebral column. The vertebral column is shown in the restoration in Text-figure 23. It consists of approximately 70 vertebrae although the number is slightly variable, some specimens appearing to have up to 73, although none has less than 70. Of these 70 or so vertebrae 30 are caudal. The centra are longest in the anterior precaudal region and decrease in length posteriorly, those of the caudal region being uniform in size with the length of each centrum just in excess of its depth. In the anteriormost precaudal region the centra are at least twice as long as deep. All of the centra are mesially constricted and in the precaudal region this is especially noticeable. The characteristic feature of the precaudal region is the possession of prominent laterally directed transverse processes on each centrum. On the first few precaudal centra the transverse processes are relatively short and broad based, and borne on the anterior region of each centrum. Pleural ribs appear to articulate with the undersurface of each transverse process. The size of the transverse processes is constant back to about the 20th precaudal vertebra where they begin to elongate and incline slightly forwards. Thus while the centra decrease in length the transverse processes increase so that the longest transverse process, on the 35th precaudal vertebra, is just longer than the centrum supporting it. The transverse processes rapidly decrease in length and incline ventrally to fuse together and produce a haemal arch by the 40th vertebrae. Neural arches occur on all the vertebrae and are long and low. The neural spines arising from the arches are abbreviated and insignificant anteriorly but become more prominent towards the caudal region. The neural spines are straight. The neural arches occupy the whole of the dorsal extent of the corresponding centra, the neural spines being produced from the posterior end of each arch. Haemal arches and spines characterise the caudal region. The haemal spines remain small and feeble but, unlike the neural spines, exhibit a marked posterior curvature. The pleural ribs which articulate with the transverse processes are long and thin and directed posteriorly,

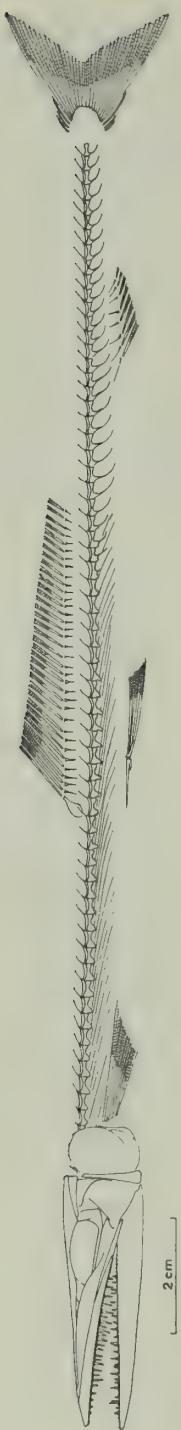


FIG. 23. *Dercetis triqueter* Pictet. Restoration of the skeleton, scales omitted.

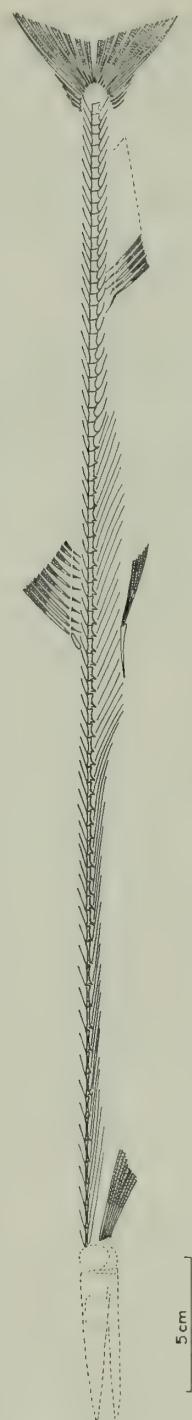


FIG. 24. *Dercetis armatus* (von der March). Restoration of the skeleton, scales omitted.

curving only slightly towards the ventral region. Thus an elongated, extremely thin 'neck' region is produced, only appearing to widen near the dorsal and pelvic fins. The region below the vertebral column was presumably occupied by a highly distensible stomach region. Intermuscular bones, both epineurals and epipleurals, are present along much of the body.

Median fins and tail. The median fins are shown in the restoration, Text-figure 23. The dorsal fin is elongate and composed of approximately 35 rays, occupying the mid-third of the trunk. Anteriorly the fin rays are well formed, segmented and branched, the more posterior fin rays are small and feeble but still branched and segmented. The proximal radials have a short shaft region with an expanded stellate head for the articulation of the fin rays.

The anal fin is small and remote, occurring well behind the dorsal fin and quite close to the caudal fin. Eight or 9 small rays are visible, all branched and segmented.

The caudal skeleton appears to consist of at least 3 free preural vertebrae with a distinct free ural vertebra (ural 1) and possibly a terminal half-centrum representing the remains of ural vertebra 2. Apart from these facts practically nothing can be made of the caudal skeleton. The fin itself consists of 19 principal caudal rays of which 17 are branched. Accessory fin rays above and below the caudal fin number about 12.

Scales. The body is devoid of normal squamation but there are 3 rows of enlarged basically triradiate scutes (Text-fig. 82A) along each flank. The two major rows of scutes positioned dorso-laterally and ventro-laterally are triradiate. Each scute has an elongated anterior extension and two divergent posterior extensions; the angle between the posterior arms is about 60°. The scales on the dorso-lateral part of the flank have a longer upper posterior arm which curves over on to the dorsal surface of the body approaching its fellow of the opposite side. Similarly in the ventro-lateral row the lower posterior arm is the longer and it too curves round towards the ventral surface. Intermediate, lath-shaped scutes occur in two distinct rows on the caudal region of the body, as extensions towards the mid-line of the flank from the shorter posterior arms of the major scutes. The third row of scutes which occurs along the whole length of the body is positioned on the course of the lateral line. These scutes are smaller, markedly less triradiate, elongate and heart-shaped. All of the scutes in the three major rows bear a small backwardly projecting spine arising from the angle between the two posterior arms. These spines are more pronounced and uncinate in the caudal region.

A great variability in the shape of the scutes occurs within the genus *Dercetis* and even within the species *Dercetis triqueter*, the nature of the scutes appearing to be dependent on the size of the specimen. Thus in the larger specimens the triradiate nature of the scales becomes obscured due to the expansion of the scale between each pair of arms. This expansion of the scales imparts an almost complete covering to the flank, the three major rows now practically contacting each other.

REMARKS. Two further species of *Dercetis* occur in the Sahel Alma deposits, *Dercetis gracilis* (Davis) (Text-figure 25) and *Dercetis rostralis* (Signeux) (Text-figure 26). The former is generally more fragile and smaller in size than the latter and the



FIG. 25. *Dercetis gracilis* (Davis). Restoration of the skeleton, scales omitted.



FIG. 26. *Dercetis rostralis* (Signeux). Restoration of the skeleton, scales omitted.

total vertebral count is higher (80). The scale pattern would seem to be identical to that of the smaller specimens of *Dercetis triqueter* in which no expansion of the scales has occurred. *Dercetis rostralis* (Signeux) is a much more slender species than even *Dercetis gracilis*. The precaudal region has vertebrae at least six times as long as deep. The scute arrangement in this 'neck' region is also simplified, with only a single row of scales (lateral line?), whereas in the caudal region the more typical squamation of the genus is exhibited, i.e. three rows of scales.

Genus **RHYNCHODER CETIS** Arambourg, 1944

DIAGNOSIS (emended). Dercetidae in which the rostral region of the neurocranium is excessively elongated. Rostrum formed distally of premaxillae united in the mid-line. Mandible does not reach the anterior end of the premaxillae. Maxillae long, narrow and toothed, forming half of the gape. Teeth on dentaries, maxillae, palatines and ectopterygoids, but not on premaxillae. Paired fins reduced in size, pectoral fins on mid-flank region, pelvics arise behind the origin of the dorsal fin. Dorsal fin always short and midway along the body. Anal fin always short and remote. Two pairs of transverse processes on each precaudal centrum, the ribs articulating with the anterior pair. Dermal scutes reduced to a single row on each flank along the lateral line.

TYPE-SPECIES. *Rhynchodercetis yovanovitchi* Arambourg.

REMARKS. The genus was erected by Arambourg (1944) to contain the single species *Rhynchodercetis yovanovitchi*, which is abundant in the Lower Cenomanian deposits of Morocco. Arambourg (1954) later expanded his original descriptions using new and more complete material from Morocco. *Rhynchodercetis* material from other localities is not abundant : *Rhynchodercetis yovanovitchi* has been described from Sicily by Leonardi (1966) ; *Rhynchodercetis gortanii* from Comen by d'Erasmo (1946) ; and *Rhynchodercetis hakelensis* from Hakel by Pictet & Humbert (1866).

Rhynchodercetis hakelensis (Pictet & Humbert)

(Text-figs. 27, 28)

1866 *Leptotrachelus hakelensis* Pictet & Humbert : 98, pl. 14, fig. 3.

1901 *Leptotrachelus hakelensis* Pictet & Humbert ; Woodward : 184.

DIAGNOSIS (emended). *Rhynchodercetis* of up to 10 cm. in standard length. Vertebral column with approximately 60 vertebrae of which 30 are caudal. Head length equal to one-quarter of the standard length. Maximum height of the head equal to one-fifth of the total head length. Preorbital length of the head forming 70% of the total. Dorsal fin with 7 rays, anal fin with 8 rays.

HOLOTYPE. Minute, incomplete fish in the Museum d'Histoire Naturelle, Geneva, from the Middle Cenomanian, Hakel, Lebanon.

MATERIAL. One specimen, number P.6001 in the B.M.N.H., prepared by the transfer method. The specimen is poorly preserved as are the other minute specimens in the B.M.N.H.

DESCRIPTION. *Neurocranium.* The neurocranium is shown in dorsal view in Text-figure 27. It is elongate and relatively shallow, and with an acutely pointed, elongated anterior region. The widest point of the skull-roof is immediately posterior to the orbits and is represented by the lateral extension of the sphenotics. The major part of the skull-roof is composed of frontals which extend almost back to the occipital border. The bones are relatively smooth, only bearing a few weak ridges which indicate the course of the sensory canals. The presence or absence of a post-temporal fossa is difficult to determine, but in the postero-lateral region of the neurocranial roof there is a definite groove which may represent an unroofed post-temporal fossa. More anteriorly, however, the frontal is flat and perhaps indicates that if the fossa extended into this region then it was roofed. The frontals meet in the mid-line and extend backwards to cover the anterior regions of both the supraoccipital and the parietals. The supraoccipital thus separates the parietals in the mid-line. The supraoccipital bears a prominent posteriorly directed crest which does not rise above the plane of the skull-roof. The frontals form the upper margins of the orbits and taper anteriorly to insert on to the posterior edges of the mesethmoid. The mesethmoid is a long bone composed of two slightly divergent posteriorly directed limbs. The frontals are inserted between these projections,

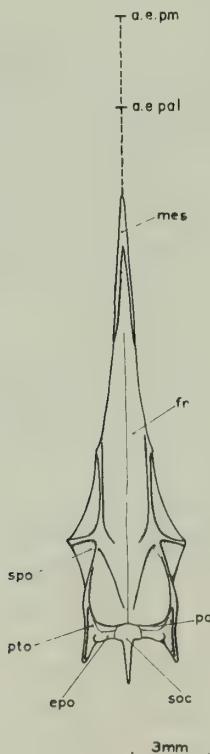


FIG. 27. *Rhynchodercetis hakelensis* (Pictet and Humbert). Neurocranium in dorsal view.

attaching to their medial edges. (A nasal component was not observed in the specimen and it may be that it is co-ossified with the mesethmoid.) The mesethmoid continues anteriorly in advance of the frontals and ends in an acute point. The supraorbital sensory canal ran within the frontal. In the snout region the sensory canal appears to have been directed towards the lateral region of the mesethmoid (possibly supporting the assumption that a nasal component is present in the mesethmoid). The infraorbital sensory canal crossed the dorsal surface of the sphenotic beneath the lateral flange of the frontal and joined with the otic branch of the infraorbital sensory canal. This latter branch passed on to the dorsal surface of the sphenotic.

The pterotic is an elongate bone forming the postero-lateral border of the skull-roof, and bearing a shallow longitudinal crest inclined medially anteriorly. The otic branch of the infraorbital sensory canal passed within this crest and anteriorly the tube for the canal is clearly visible. Posteriorly the pterotic projects backwards for a considerable distance beyond the occipital border. Ventro-laterally the pterotic forms most of the hyomandibular facet. The pterotic contacts the sphenotic anteriorly, and the sphenotic contributes towards the anterior region of the hyomandibular facet. Postero-medially the pterotic joins the epiotic and parietal in the open groove which may represent the post-temporal fossa. The epiotic is poorly shown but does exhibit a slight thickening medial to the groove which provided an articulatory area for the dorsal limb of the post-temporal.

The parasphenoid is visible below the orbit and is considerably expanded into ventro-lateral flanges which presumably were associated with the medial edges of the endopterygoids. The lateral ethmoid delimits the anterior orbital region and is a large bone attached ventrally to the postero-dorsal region of the palatine.

Jaws and suspensorium. The jaw suspensorium is inclined slightly forwards ventrally so that the quadrate condyle is positioned below the centre of the post-orbital part of the skull. The head of the hyomandibular is considerably elongated, and its rear edge bears a shallow crest against which the anterior edge of the pre-operculum rested. Approximately one-third of the way down the bone this crest is joined by a second crest from the anterior region of the hyomandibular head. The combined crest so produced shallows and disappears at the ventral extremity of the hyomandibular. The anterior extent of the hyomandibular is a thin sheet of bone which is covered by the metapterygoid. The quadrate is triangular and stout with the condyle directed antero-ventrally. Anteriorly the quadrate is attached to the lateral face of the ectopterygoid. The association of the quadrate with the metapterygoid is difficult to interpret, the latter appearing to overlap part of the hyomandibular and to bear an obliquely inclined crest anteriorly. The ectopterygoid expands slightly below the orbit where it is more thickened and prominent. It is assumed that this region ventrally bears teeth although none were clearly observed. Further forwards, below the lateral ethmoid, the ectopterygoid contacts the postero-ventral part of the palatine. An endopterygoid is attached to the medial region of the ectopterygoid and is inclined medially to associate with the parasphenoid in the roof of the mouth. The palatine is excessively elongated, deepest posteriorly and

tapering in height anteriorly. Postero-dorsally it is supported by the ventral region of the lateral ethmoid, and more anteriorly it is associated medially with the lateral parts of both the mesethmoid and vomer. Anteriorly the palatines continue in advance of the mesethmoid and meet in the mid-line, terminating anteriorly in an acute point. Traces of teeth are seen along the length of the palatine.

The dermal upper jaw is composed of two bones, the premaxilla and the maxilla. Each bone appears to contribute about half of the oral margin of the upper jaw. The premaxillae are produced for a considerable length in advance of the end of the palatines, and also meet in the mid-line. The premaxillae lie lateral to the palatines and have a smooth external surface. No traces of teeth are visible on the premaxillae. Only the posterior region of the maxilla is visible, i.e. where it enters the gape, and the anterior extent cannot be ascertained. The maxilla is a relatively shallow lamina of bone bearing a row of minute teeth.

The mandible is long and very shallow, and only extended as far as the anterior end of the palatines. The articular facet is shallow and ill-defined and there is no distinct coronoid process, the rear edge of the articular merely sloping forwards to contact the dentary. The dentary is deeply indented posteriorly and this indentation is occluded by the forward extent of the articular. A small angular element occurs below the articular facet. A lateral flange, running in a longitudinal direction, is present on the articular bone; when the jaws are closed the posterior end of the maxilla rests on the dorsal surface of this flange. Orally the dentary bears traces of teeth. No ornamentation occurs on the lower jaw.

Opercular bones. The preoperculum is inclined forwards ventrally where it is associated with the rear edge of both the hyomandibular and the quadrate. It is a narrow bone with a slight ventral expansion. The operculum is very large and is as deep as it is long with no ornamentation. The suboperculum is as long as the operculum but is considerably shallower and its dorsal region lies medial to the ventral region of the operculum. An interoperculum is not present.

Fins and fin supports. The fins are shown in the reconstruction, Text-figure 28. The pectoral girdle is hardly visible in the specimen, only traces of the cleithrum can be seen behind the opercular apparatus. The cleithrum is narrow with a considerable vertical and horizontal extent, following the contour of the rear edge of the opercular bones. The pectoral fin insertion is high up on the flank, above the mid-line of the body. The fin consists of at least 10 branched and segmented rays.

The pelvic bones are narrow fragile slips of bone positioned below the middle of the dorsal fin. The pelvic fin rays are feeble but all are branched and segmented, totalling at least 7 in number.

The dorsal fin is short but relatively deep, the first two or three rays being longer than the basal length of the fin. The fin consists of about 6 rays which are relatively stout, though flattened, and only appear to be segmented at their extreme distal ends. The radial elements supporting the fin rays are short with an expanded articulatory region. The first radial also bears a slight anterior expansion.

The anal fin is composed of at least 8 rays and is remote in position.

Vertebral column. The vertebral column is shown in the reconstruction, Text-figure 28. It consists of approximately 60 vertebrae, of which 30 appear to be caudal. The first 18 precaudal vertebrae are of uniform size, as long as deep. Between the 18th and the 22nd a slight increase in vertebral length occurs but after the 22nd the centra remain constant with a length slightly in excess of their depth. The length of each vertebra decreases in the region of the 20th caudal vertebra. Each centrum is mesially constricted and on the longer centra the constriction is most noticeable. The characteristic feature of the precaudal region is the presence on each centrum of two pairs of prominent transverse processes. The processes are directed ventro-laterally and occur at either end of the centrum. The anterior transverse process is larger than the posterior. The processes remain relatively constant in size on the first 15 precaudal vertebrae, but posterior to this they begin to elongate and reach their greatest length at about the 22nd precaudal vertebra, i.e. below the origin of the dorsal fin. Posterior to the 22nd vertebra the transverse processes gradually decrease in length and incline more ventrally. In the caudal region the anterior pair of transverse processes fuses ventrally to produce the haemal arches whilst the posterior pair appears to become zygapophyses. Ribs if present are very feeble and short, one or two centra do appear to have small fine ribs articulating with the underside of the larger, anterior, transverse processes. Long and low neural arches are present along the entire length of the column. Each neural arch occupies the whole dorsal extent of the corresponding centrum and gives rise to a feeble, posteriorly directed neural spine. These spines arise from the posterior region of each neural arch, and a prominent prezygapophysis is visible on the anterior region. The entire length of the body seems to have been provided with intermuscular bones, both epineurals and epipleurals, and possibly a certain number of epicentrals. Along a considerable part of the precaudal region in the mid-dorsal line there are several ossifications which are more substantial than the intermuscular bones. These may represent several median intermusculars compounded together, or, more probably, an ossified dorsal ligament. Just behind the occipital region of the head the anteriormost ossification appears to expand ventrally and connects with the neural spine of the first vertebra.

Scales. The body is devoid of scales except for a single row on each flank, marking the course of the lateral line. All of the scales are based on a triradiate plan with a long forwardly projecting arm and two shorter divergent backwardly projecting arms. The interspaces between the smaller arms and the larger arm are variously filled with bone to give a more rounded outline which becomes more noticeable caudally. At the point of junction of the three arms a small backwardly projecting spine occurs: this is present on all the scales but is more pronounced and uncinate in the caudal region.

REMARKS. Arambourg's (1954) description of the type species *Rhynchodercetis yovanovitchi* (Text-fig. 29) differs in a few details from the above description of *Rhynchodercetis hakelensis*. Arambourg's supraorbital above the posterior end of the orbit does not appear to be a separate bone but merely the lateral extension of the frontal above the orbit. Here, as in specimens of other genera examined

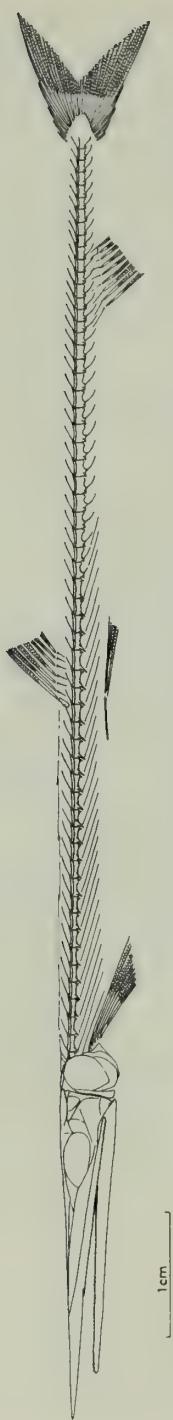


FIG. 28. *Rhynchodercetis haleensis* (Pictet and Humbert). Restoration of the skeleton, scales omitted.



FIG. 29. *Rhynchodercetis yovanovitchi* Arambourg. Restoration of the skeleton, scales omitted.

(notably *Ichthyotringa delicata*, Text-fig. 5, p. 14), the tube within the frontal which contained the supraorbital sensory canal passes medially from above the sphenotic and then curves anteriorly to pass along the dorsal surface of the frontal above the orbit. This tube often appears to demarcate the medial frontal region from the lateral frontal region, the lateral region thus having the appearance of a separate bone. Arambourg (1954 : 108) also described and figured separate nasals. I was unable to find these as discrete elements in *Rhynchodercetis hakelensis*, where they appear to have become incorporated with the mesethmoid or lost altogether, both situations occurring in other teleosts. The mandible does not always terminate at the posterior end of the premaxillae as Arambourg indicated for *Rhynchodercetis youvanovitchi*. In certain of his specimens it definitely extends further anteriorly, almost to the end of the rostrum in fact, thus agreeing with *Rhynchodercetis hakelensis* in which the mandible extends to the anterior end of the palatine. Finally Arambourg (1954 : 111) describes and figures a prominent interoperculum. I was unable to find this bone in any of his specimens and it does not appear to be present in *Rhynchodercetis hakelensis*.

***Rhynchodercetis gortanii* (d'Erasmo)**
(Text-figs. 30A-C)

1946 *Leptotrachelus gortanii* d'Erasmo : 76, pl. 1, fig. 4.

1946 *Leptotrachelus* sp. (cfr. *L. hakelensis*) d'Erasmo : 82.

1952 *Rhynchodercetis acutissimus* d'Erasmo : 108, text-figs. 7-12, pl. 2, figs. 4-6, pl. 3, figs. 1-4.

DIAGNOSIS (emended). *Rhynchodercetis* of estimated standard length up to 22 cm. Vertebral column with 78-80 vertebrae of which 30 are caudal. Head equal to between a quarter and a third of the standard length. Maximum height of the head equal to one-sixth of the total head length. Dorsal fin with 8 rays, anal fin with 16-20 rays. Pectoral fin with 10 rays, pelvic midway between the pectoral and the anal and composed of 8 rays.

HOLOTYPE. The holotype of *Leptotrachelus gortanii* d'Erasmo, once in Bologna, could not be traced. The holotype of *Rhynchodercetis acutissimus* d'Erasmo is in the Museo Civico di Storia Naturale, Trieste. Both specimens come from the Lower Cenomanian of Comen, near Trieste.

MATERIAL. Two trunk fragments from Comen in the Istituto di Geologia e Paleontologia della Università, Bologna ; specimen number P.10913 in the B.M.N.H. ; and an incomplete specimen from the Natural History section, Prirodoslovni Muzej Slovenije, Ljubljana, Jugoslavia.

REMARKS. *Leptotrachelus gortanii* was erected by d'Erasmo (1946) on a practically complete specimen from Gabrovizza in Comen, near Trieste. Together with the holotype d'Erasmo also used two trunk fragments from Dol Piccolo, also in Comen. The author has examined these latter specimens in Bologna but the holotype is missing. The holotype of *Rhynchodercetis acutissimus* d'Erasmo (1952) together with several other body fragments, all from Comen, are in Trieste. Unfortunately these specimens were not made available to me but subsequently photographs of this

material have been studied. The original descriptions of d'Erasmo (1946; 1952) together with the body fragments in Bologna have convinced me that only one species is represented. A small head region, also from Comen, in Bologna, was noticed by d'Erasmo (1946: 82). He ascribed this specimen to the genus *Leptotrachelus*, and indicated that it had affinities with the species *Leptotrachelus hakelensis*. It almost certainly is a specimen of *Rhynchodercetis gortanii*.

Due to the lack of material, only a few features are described. All the features are well shown by the two specimens from Comen, one in the B.M.N.H. number P.10913, and the other in Ljubljana. Both specimens are of the mid-trunk region and exhibit both precaudal and caudal vertebrae.

DESCRIPTION. *Vertebral column.* Selected vertebrae are shown in Text-figures 30 A-C. Approximately 59 vertebrae are exhibited in the Ljubljana specimen, of which 39 are precaudal. (The type specimen of *Rhynchodercetis acutissimus* has 80 vertebrae in all, of which 30 are caudal.) Anterior to the dorsal fin the specimen is flattened dorso-ventrally due to the prominent transverse processes having prevented twisting of the body during fossilization. However further back the dorsal fin and the pelvic fins have overridden this effect and the remainder of the body is preserved normally by lateral compression. The body was obviously long and very thin, and the precaudal region is characterized by the presence of two pairs of

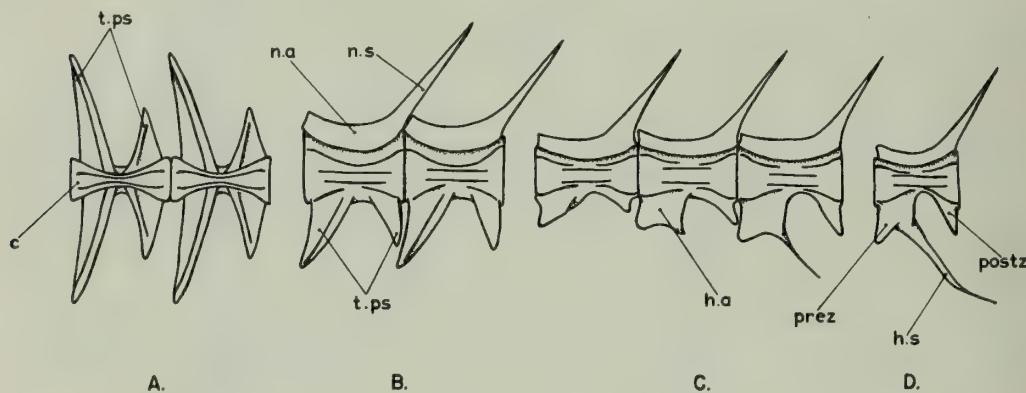


FIG. 30. *Rhynchodercetis gortanii* (d'Erasmo). Selected vertebrae. (A) Ventral view of precaudal vertebrae 26 and 27. (B) Lateral view of precaudal vertebrae 42 and 43. (C) Lateral view of precaudal vertebra, 50 and caudal vertebrae 1 and 2. (D) Lateral view of caudal vertebra 15.

enormous transverse processes per centrum. The transverse processes are long and acutely pointed, but are flattened and extended where they contact the centrum. The anterior pair of transverse processes is almost twice as long as the posterior pair. The length of the anterior processes increases posteriorly and they attain their greatest length at about the 26th precaudal vertebra, (i.e. assuming that 80 vertebrae are present of which 50 are precaudal). The greatest length of the anterior transverse processes is in excess of the length of the centrum supporting them. The posterior pair of transverse processes are set at 90° to the long axis of the centrum

whereas the anterior processes incline slightly forwards. Pleural ribs articulate with the apices of the larger pair of transverse processes. Some of the smaller, posterior transverse processes appear to have thin bones articulating with them, but these are more likely to be some of the numerous intermuscular bones. Posterior to the 26th precaudal vertebra both the pairs of transverse processes begin to decrease in length so that by the end of the precaudal region, at about the 50th vertebra, the processes are much reduced and project ventrally as opposed to their more normal ventro-lateral inclination. The anterior pair of transverse processes fuses in the mid-ventral line to produce the haemal arches ; this seems to have occurred on the 51st vertebra. From the postero-ventral part of this haemal arch a protuberance occurs which on the succeeding caudal vertebrae becomes elongated, forming curved haemal spines which attain their maximum length on the 4th caudal vertebra. As has been pointed out, the haemal spine arises from the posterior region of the haemal arch, while the anterior region of the haemal arch projects forwards very slightly on either side to form ventral prezygapophyses. The posterior transverse processes also incline ventrally in the caudal region but do not fuse together, merely forming ventral postzygapophyses. Throughout the caudal region the ventral pre- and postzygapophyses are extremely prominent. The entire length of the dorsal surface of each centrum is occupied by an elongated neural arch which is a separate ossification to the centrum, the suture between the two structures being clearly visible. The neural arches are long and low and bear neural spines as projections from the extreme postero-dorsal region. The anterior region of each neural arch is produced on either side to give prezygapophyses. The corresponding postzygapophyses are found on the postero-dorsal part of the centrum, posterior to the base of the neural spine. The neural spines themselves are not particularly prominent, being short, straight and relatively narrow.

Genus **PELARGORHYNCHUS** von der Marck, 1858

DIAGNOSIS (emended). Dercetidae in which both the skull and body are elongated. Premaxillae do not extend in front of the mesethmoid. Mandible extends to the anterior region of the snout. Maxilla enters the gape and is toothed. Paired fins reduced in size, pectorals being low on the flanks, pelvics arising below the anterior end of the dorsal fin. Dorsal fin occupies the posterior half of the back, anal fin short and remote. A single row of heart-shaped flank scutes along the lateral line, and a dense intermediate squamation of small rhomboidal scales covers the remainder of the body.

TYPE SPECIES. *Pelargorhynchus dercetiformis* von der Marck.

REMARKS. The genus was erected by von der Marck (1858) for the reception of several poorly preserved specimens from Sendenhorst, Westphalia. The genus is not recorded from any other localities.

Pelargorhynchus dercetiformis von der Marck

(Text-fig. 31)

1858 *Pelargorhynchus dercetiformis* von der Marck : 243.1954 *Pelargorhynchus dercetiformis* von der Marck ; Siegfried : 16, pl. 6, figs. 2-4.
Siegfried lists earlier references.

DIAGNOSIS (emended). *Pelargorhynchus* of standard length not exceeding 49 cm. Vertebral column with 70 vertebrae. Head equal to one-fifth of the standard length. Maximum height of the head equalling one-fifth of the total head length. Dorsal fin with 64 rays, anal fin with 13 rays. Lateral line scutes elongate and heart-shaped.

HOLOTYPE. The holotype appears to have been lost, but two additional specimens used by von der Marck (1858, 1863) are present in the Paläontologisches Institut der Westfälische Wilhelms-Universität, Münster, numbers 8488 and A1/3, both from the Upper Senonian of Sendenhorst.

MATERIAL. The two specimens in Münster together with a third specimen of a distorted trunk region in Münster. These three specimens are all that could be traced of the species. The following description is very incomplete due to the poor preservation of the material.

DESCRIPTION. *Neurocranium*. The neurocranium is shown in dorsal view in Text-figure 31. The frontals extend back almost to the occipital border and are long, narrow bones which meet in the mid-line. The widest point of the skull-roof is between the sphenotics on a level with the hind end of the orbit. The frontals are densely ornamented with rows of tubercles raised on bony ridges. These ridges radiate in all directions from the centre of ossification above the rear end of the orbit. The sphenotic is visible on one side of the roof as a triangular region projecting laterally from beneath the frontal. The frontals are greatly extended anteriorly and taper from in front of the orbits. The mesethmoid component of the skull is prominent and acutely pointed anteriorly, but more posteriorly is composed of two divergent laminae of bone flanking the anterior region of the frontals. In lateral view the orbit appears small, the majority of the skull length being preorbital. The parietals are small, transversely orientated strips of bone near to the occipital border and bounded anteriorly by the frontals. The supraoccipital is a small bone which contacts the frontals anteriorly and separates the parietals in the mid-line. A supraoccipital crest was not observed but preservation was poor in this region. Both parietals bear a dense ornamentation of tubercles but the dorsal surface of the supraoccipital is smooth. Behind the parietals and forming the occipital border of the roof, two small unornamented expanses of bone are visible, the epiotics. Postero-lateral to the frontals the pterotics border the skull-roof. The pterotics are elongate and relatively narrow although they do expand slightly in width posteriorly. The pterotic projects backwards beyond the level of the occipital border. Posteriorly a slight indentation of the pterotic is visible in the posterior border of the neurocranium just lateral to the epiotic and the parietal, and would seem to indicate the presence of a post-temporal fossa. The indentation may mark

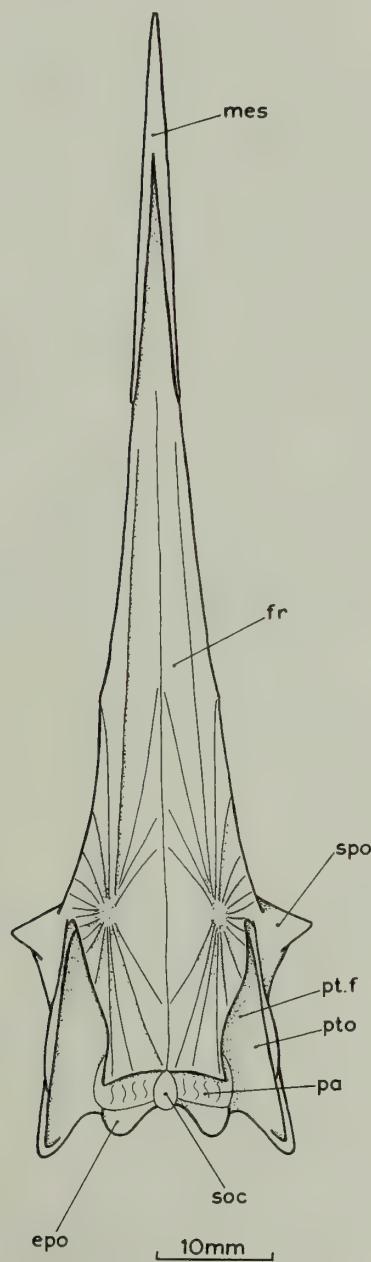


FIG. 31. *Pelargorhynchus dercetiformis* von der Marck. Neurocranium in dorsal view.

the opening of a completely roofed post-temporal fossa but is more probably the posterior portion of an unroofed or partially roofed fossa.

Jaws and suspensorium. The suspensorium is vertical with the quadrate condyle lying below the occipital border. Little of the remainder of the palate could be made out except that the palatine appears to support a double series of hollow teeth. The palatine is closely associated with the anterior end of the snout and was in part supported by the mesethmoid.

The dermal upper jaw consists mainly of an elongated, shallow premaxilla extending from the extreme tip of the snout almost to the rear of the orbit. The premaxilla appears to contact its partner anteriorly in the mid-line. The lateral surface of the premaxilla is ornamented with tuberculated ridges, and the oral margin bears a uniform row of minute teeth. The maxilla enters the gape behind the premaxilla as a thin splint of bone, bearing a single row of small conical teeth.

The mandible is elongated and very shallow with the dentary forming the whole of the oral border. The lateral face of the mandible is sparsely ornamented and the oral edge is covered with many small, acutely pointed, recurved needle-like teeth. The articular is more densely ornamented on its lateral face than the dentary and the facet for the reception of the quadrate condyle is shallow and ill-defined.

The preoperculum is upright, narrow and with a slight basal expansion. The operculum is large and has a rounded posterior edge, whilst the suboperculum is much smaller. There are numerous branchiostegal rays in the region of the suboperculum, but it would appear that the interoperculum was absent.

Vertebral column and fins. The body is of a characteristic shape, the neck region being constricted and of no greater depth than the maximum depth of the head. The body widens gradually and attains its maximum depth at the level of the pelvic fin. The vertebral column is composed of approximately 70 vertebrae, the individual centra are mesially constricted and in the anterior region of the body are longer than they are deep. The centra decrease both in height and length as they near the caudal extremity. Apart from this little can be said concerning the vertebral column due to the complete covering of scales which masks the underlying structures.

The pectoral fins are positioned quite low down on the flank and appear to consist of some 12 rays. The pelvic fins are larger and positioned midway along the body beneath the 32nd vertebra, and have about 7 rays, the first of which is unbranched. The dorsal fin occupies practically half of the length of the body and is composed of 64 rays. The anal fin is remote in position with 13 rays, opposite the hind end of the dorsal fin. The caudal fin is prominent but not deeply cleft and consists of 19 principal rays and approximately 12 accessory rays.

Scales. The whole body is covered with a complete coat of small imbricate scales which are rhomboidal in shape. Along the course of the lateral line the scales are much enlarged, elongate and heart-shaped. Each lateral line scute bears a small posteriorly directed spine and an ornamentation of radiating tubercles. There might possibly be a second row of enlarged scutes on the body but this is not definite, despite Woodward's (1901 : 188) statement.

Suborder ENCHODONTOIDEI

DIAGNOSIS. Body relatively shallow and somewhat laterally compressed. Parietals separated completely by the supraoccipital; post-temporal fossa roofed or unroofed. Orbitosphenoid and basisphenoid absent. Supraorbital and antorbital absent. Premaxilla with a fenestrated pedicel; maxilla untoothed or finely toothed; supramaxillae absent. Palatine bone thick and tumid with a terminal palatine tooth; teeth absent on the vomer. Large number of branchiostegal rays. Interoperculum absent. Pectoral fins inserted low down on the flank; no mesocoracoid arch. Pelvic fins abdominal or sub-thoracic. Vertebral elements incompletely fused; epineurals present. Vertebrae variable in number, more than half the total being caudal. Fins without spines; caudal with 19 principal fin-rays, 17 branched. Caudal skeleton with second ural vertebra present as a half-centrum. Scales present only along the lateral line and the mid-dorsal line anterior to the dorsal fin.

Family ENCHODONTIDAE Woodward, 1901

DIAGNOSIS (emended). Head deepened, especially posteriorly; body may be deepened in thoracic region. Post-temporal fossa unroofed. Lower jaw long and deep behind the constricted symphysis; articular facet visible from the lateral aspect. Operculum convex posteriorly and deeper than it is broad; preoperculum without prominent ventral spine. Pectoral fins larger than pelvic fins and extremely low on body. Pelvic fins abdominal. No posterior extension of the cleithrum. Lateral line scales do not overlap; mid-dorsal scutes reduced and not overlapping.

Genus ENCHODUS Agassiz, 1835

DIAGNOSIS (emended). Enchodontidae in which the body tends to become shortened and deepened. Vertebral number may be reduced to 37, caudal region remaining relatively constant at 25 vertebrae. Pectoral fins only slightly larger than pelvic fins. Anal fin short based, arising behind dorsal fin. Dorsal fin short based and in the middle of the back. Mid-dorsal scutes reduced and few in number.

TYPE SPECIES. *Enchodus lewesiensis* (Mantell)

REMARKS. The genus *Enchodus*, first erected by Agassiz (1835), is known by many species. The majority have been erected on fragmentary material consisting mainly of isolated teeth or fragments of the jaw bones (see Woodward 1901 : 190-205). Only a few species are represented by complete material and two of these are described in the following pages. The neurocranium and jaws of *Enchodus fajasi* Agassiz have been described in detail by Goody (1968).

Enchodus lewesiensis (Mantell)

(Text-figs. 32-36, 38A)

- 1822 *Esox lewesiensis* Mantell : 237, pl. 25, fig. 13, pl. 33, figs. 2-4, pl. 41, figs. 1-2.
 1835 *Enchodus halocyon* Agassiz, Feuill. : 55.
 1837 *Enchodus halocyon* Agassiz, 5 ; 1 : 64, pl. 25c, figs. 1-16.
 1850 *Enchodus halocyon* Agassiz ; Dixon : 373, pl. 30, figs. 20 & 27, pl. 31, fig. 11.
 1875 *Enchodus halocyon* Agassiz ; Geinitz : 226, pl. 41, figs. 5-20 (*partim*).
 1883 *Enchodus lewesiensis* (Mantell) Sauvage : 480, pl. 12, fig. 16.
 1883 *Enchodus halocyon* Agassiz ; Gosselet : pl. 22, fig. 1.
 1888a *Enchodus lewesiensis* (Mantell) ; Woodward : 315, pl. 1, fig. 5.
 1901 *Enchodus lewesiensis* (Mantell) ; Woodward : 191, pl. 11, fig. 1.
 1901 *Enchodus annectens* Woodward : 195, pl. 11, figs. 4 & 5.
 1902 *Enchodus lewesiensis* (Mantell) ; Leriche : 139, pl. 4, fig. 13.
 1903 *Enchodus annectens* Woodward ; Woodward : 57.
 1903 *Enchodus lewesiensis* (Mantell) ; Woodward : 57, pl. 14, figs. 1-8, text-fig. 13.
 1906 *Enchodus lewesiensis* (Mantell) ; Leriche : 95, text-fig. 15.
 1908 *Enchodus lewesiensis* (Mantell) ; Priem : 52, pl. 1, fig. 10, pl. 2, fig. 2.
 1930 *Enchodus annectens* (Woodward) ; Maury : 99, fig. 4.
 1932 *Enchodus lewesiensis* (Mantell) ; Woodward : 160, fig. 246.
 1933 *Enchodus lewesiensis* (Mantell) ; Sarra : 30.
 1937 *Enchodus lewesiensis* (Mantell) ; Rode : 127, pl. 9.
 1964 *Enchodus lewesiensis* (Mantell) ; Danil'chenko : 411, fig. 127.

DIAGNOSIS (emended). *Enchodus* in which the length of the head exceeds its depth at the occiput ; maximum depth of the body behind the occiput estimated as equal to the length of the head. Dermal bones of the head ornamented with radiating tuberculated ridges. Mandibular teeth six in number of which the anteriomost is the longest ; both hyopalatine and mandibular teeth long, thin and needle-like. Palatine tooth fractionally longer than the first tooth on the ectopterygoid. Mandibular symphysis much constricted ; mandible deepens posteriorly so that the maximum depth is equal to one-third of its total length. Maxilla long and thin and probably untoothed.

SYNTYPES. Specimens in the B.M.N.H., numbers 4004, 4049, 4157, 4160, 4180, 4181, 4183, 4184, 4198, being a collection of teeth and jaw fragments from the Turonian and Senonian of south-east England.

MATERIAL. Specimens in the B.M.N.H. totalling some 20 fragmentary pieces, listed by Woodward (1901 : 192).

REMARKS. The type species is only known by imperfect specimens of the head. The series of type specimens are those figured by Mantell (1822) and Agassiz (1837), all from the Chalk of Sussex. The following description is based mainly on specimen number 4001 in the B.M.N.H. from the Middle Chalk of Lewes in Sussex, described by Woodward (1901 : 192) as a very imperfect small skull. The specimen was prepared in acetic acid and a small practically complete neurocranium was obtained. The description of the jaws was compiled from several fragmentary specimens, notably specimen number P.5415 which had already been partially described and figured by Woodward (1888a : 315, pl. 1, fig. 5).

DESCRIPTION. *Neurocranium.* Dorsal, ventral, lateral and posterior views of the neurocranium are shown in Text-figures 32–35. The cranial roof is flattened with its widest point behind the orbits in the sphenotic region. The cranium is relatively deep in the posterior region but shallower anteriorly. The orbit is enormous, occupying more than half the length of the neurocranium, whilst the cranial cavity itself is very small.

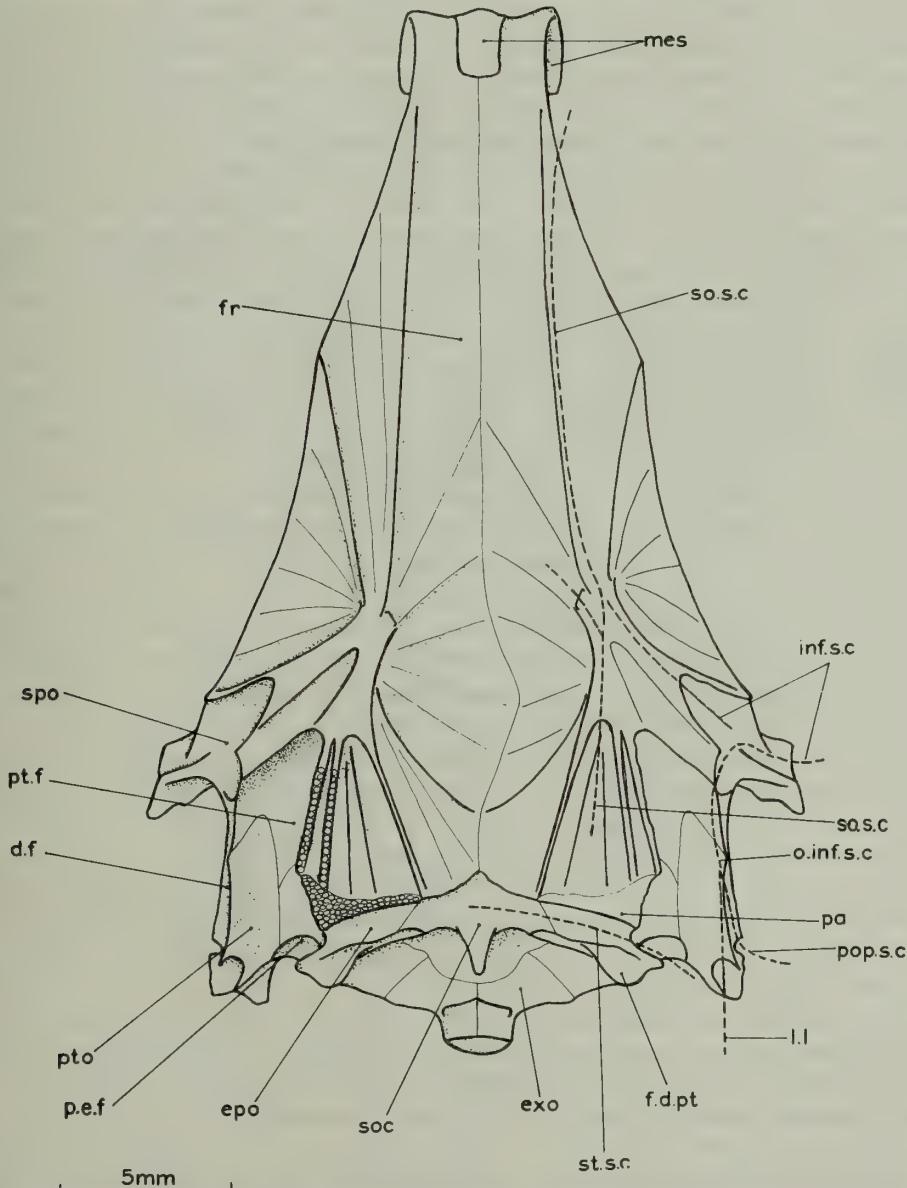


FIG. 32. *Enchodus lewesiensis* (Mantell). Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals.

The frontals form almost the whole of the skull-roof, meeting in the mid-line in a distinct suture. A deviation of the suture to the right side of the roof is very noticeable in the posterior third of the frontal region. Posteriorly the frontals end near to the occipital border overlapping the anterior regions of the remainder of the roofing bones. The medial region of the roof is flat and relatively unornamented, and between the orbits there is a slight inter-orbital depression. The more lateral region of each frontal bears extremely prominent ridges which run in longitudinal and lateral directions from the centre of ossification. The major ridges bear an ornamentation of small bony tubercles. Several of the most prominent ridges pass forwards towards the snout region ; others pass laterally to terminate on the upper margin of the orbit. The ridges which extend posteriorly are arranged into a fan, the most lateral ridge passes straight back along the upper margin of the internal wall of the post-temporal fossa while the most medial ridge passes in towards the mid-line. The postero-lateral region of each frontal displays a V-shaped indentation of the upper ornamented layer. This indentation marks the forward extension of the unroofed post-temporal fossa. The frontal itself extends into the fossa forming the anterior regions of both the medial and lateral walls as well as the floor. The posterior half of the fossa is composed medially of parietal and laterally of pterotic. The frontal is applied to the dorsal surface of the sphenotic, this latter bone producing the upper hind limit of the orbit. Anteriorly the frontals taper from the orbits and contact the mesethmoid.

The supraoccipital appears on the surface of the neurocranium as a small median bone with its anterior region overlain by the backward extension of the frontals, thus separating the parietals. Its internal extent is probably far greater than the outward appearance would indicate. As well as contacting the frontals and parietals, it also contacts the epiotics postero-laterally and the exoccipitals on the posterior face of the neurocranium. The supraoccipital crest is small, arising from the posterior face and not extending above the level of the skull-roof. On the surface of the supraoccipital, anterior to the origin of the crest, there is a shallow transverse groove crossing the complete width of the bone.

The parietals are composed of two distinct regions, an anterior roughly triangular portion which is heavily ornamented and closely associated with the frontals ; and a smaller postero-lateral portion which is smooth and unornamented. In this posterior, smooth region, the epiotic and parietal join in the floor of a distinct transverse groove. The grooves are continuous with the transverse groove on the supraoccipital. Laterally the parietal forms the posterior half of the medial wall of the post-temporal fossa.

The pterotic appears on the skull-roof lateral to the posterior region of the frontal. Anteriorly the pterotic is covered by a lateral extension of the frontal in the region of the post-temporal fossa. The pterotic is produced into a prominent vertical crest which forms the lateral wall and floor of the post-temporal fossa, and also part of the medial wall of the dilatator fossa. The pterotic contacts the sphenotic anteriorly and the suture is visible within the dilatator fossa. On the postero-dorsal edge of the pterotic crest a large foramen leads into a tube within the pterotic crest. A

distinct transversely orientated oval fenestra is present at the hind end of the post-temporal fossa. This enters the neurocranium beneath the post-temporal fossa, and is bordered medially by parietal and epiotic and laterally by pterotic. The possible significance of this oval fenestra entering the cranial cavity is considered by Goody (1968 : 225). The pterotic crest bears a notch and a groove postero-laterally just in front of the hind end of the crest, the groove orientated postero-ventrally. The dilatator fossa, which housed the dilatator muscle of the operculum, is a vertically arranged facet produced by excavations of the sphenotic anteriorly and the pterotic posteriorly. The dilatator fossa is lateral in position and below it is the hyomandibular facet. This latter is an elongated facet consisting of a straight groove arising anteriorly on the sphenotic and being continued posteriorly on the pterotic. The pterotic therefore contacts the sphenotic anteriorly within the dilatator fossa and the hyomandibular facet.

The sphenotic enters into the composition of the skull-roof and also forms the postero-dorsal corner of the orbit. Dorsally it projects laterally from beneath the frontal, and the surface is unornamented. The posterior surface of the lateral projection is excavated somewhat to produce the anterior end of the dilatator fossa. From the outermost region of the lateral extension a stout strut passes ventro-medially to meet a corresponding upward strut from the prootic. The anterior end of the hyomandibular facet is located behind this strut and below the dilatator fossa. In the orbit the sphenotic produces the major part of the hind wall, contacting the prootic ventrally, the pleurosphenoid medially and the frontal dorsally. The main infraorbital sensory canal crossed the dorsal surface of the sphenotic on which it appears to have connected with the otic branch of the infraorbital canal from the pterotic.

The epiotic forms the postero-dorsal part of the cranial roof medial to the post-temporal fossa. The epiotics are separated in the mid-line by the supraoccipital and they contact the parietals anteriorly within the transverse groove already noticed. Postero-dorsally the epiotic is in the form of a raised rounded knob of bone which provided the articulatory surface for the dorsal limb of the post-temporal. On the posterior face of the skull the epiotic meets the supraoccipital and exoccipital medially and the intercalar ventrally. Within the extreme posterior end of the post-temporal fossa the epiotic contacts the parietal and pterotic where these three bones form the borders of the small oval fenestra entering the cranium below the post-temporal fossa.

The supraorbital sensory canal ran in a tube of bone within the frontal, opening anteriorly on the edge of the frontal behind the mesethmoid region. Two subsidiary branches of the main supraorbital sensory canal arose from the main canal in the region of the centre of ossification. One branch passed antero-medially and opened on to the interorbital region of the roof ; the second passed postero-medially and opened on to the posterior surface of the frontal, from where it appears to have continued on the surface towards the parietal. The infraorbital sensory canal passed across the dorsal surface of the sphenotic within the groove present on that bone. It entered the lateral region of the frontal just posterior to the centre of

ossification. The otic branch of the infraorbital sensory canal probably connected with the main infraorbital canal within the frontal, or possibly on the dorsal surface of the sphenotic. It entered the foramen at the posterior end of the pterotic crest and passed anteriorly within the crest. The notch and subsequent groove seen on the postero-lateral region of the pterotic crest probably indicate the point at which

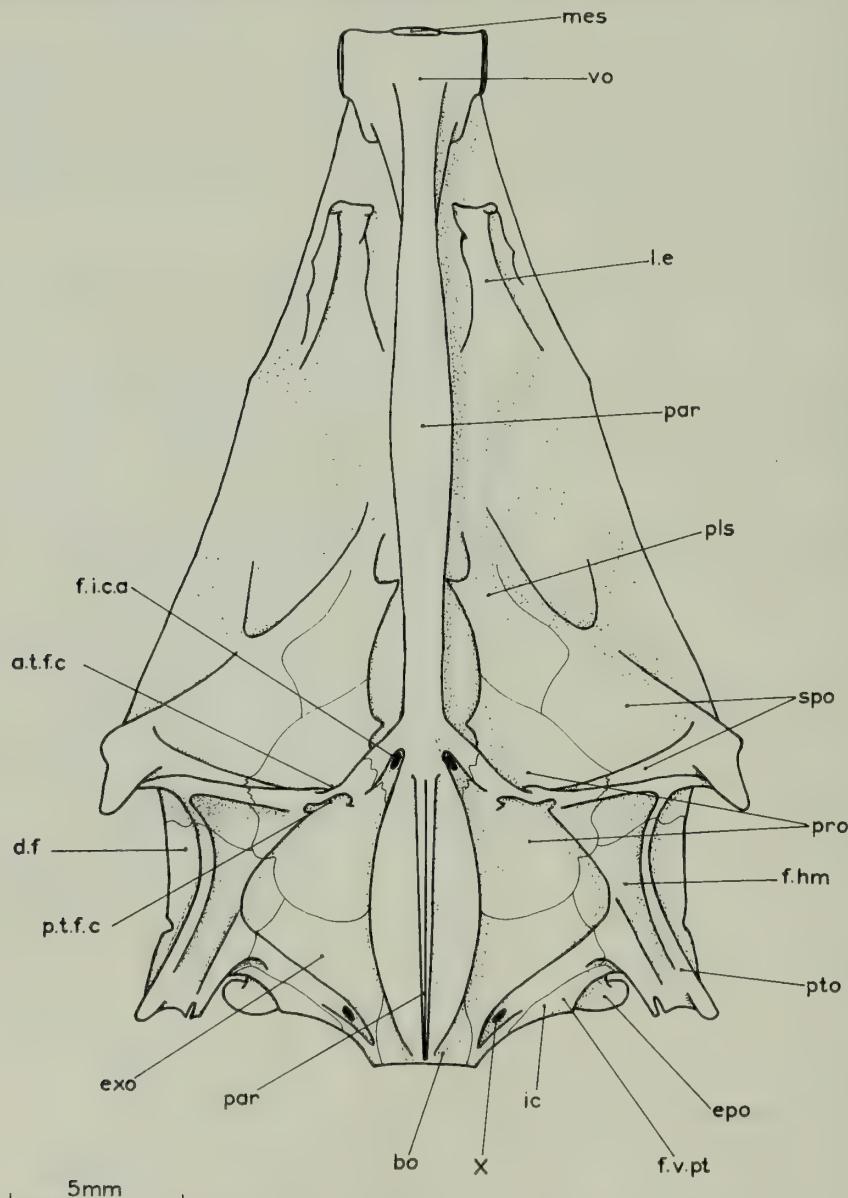


FIG. 33. *Enchodus lewisiensis* (Mantell). Neurocranium in ventral view.

the preopercular sensory canal entered the pterotic to contact the otic branch of the infraorbital canal. The presence of a complete supratemporal commissure is indicated by the continuous transverse groove on the parietals and epiotics and the supraoccipital. This groove ends laterally above the posterior end of the posttemporal fossa. Possibly the sensory canal passed laterally in a superficial position and joined with the otic branch of the infraorbital canal immediately posterior to the pterotic crest.

The mesethmoid is prominent and well ossified, bearing a pair of lateral wings which are fused to the dorsal surface of the vomer. The composite wings thus formed produce an elongate articulatory region which fits into a correspondingly elongated facet on the internal face of the anterior palatine region. The anterior edge of the mesethmoid is straight and transversely arranged. The pedicels of the premaxillae rested upon this edge.

The lateral ethmoids are well ossified both posteriorly and ventrally. The ventral region is pitted and excavated and was in life probably capped by cartilage. This region of the lateral ethmoid supported the posterior end of the palatine. Dorsally the lateral ethmoids are splayed apart and attach to the underside of the frontals.

The vomer is closely adherent to the ventral surface of the mesethmoid, although its actual outline is difficult to determine. Teeth are definitely not present on the vomer.

The parasphenoid is continuous for practically the entire length of the neurocranium. The ascending processes of the parasphenoid are inclined at 90° to the rest of the bone. Throughout the orbital region the parasphenoid is of uniform shape

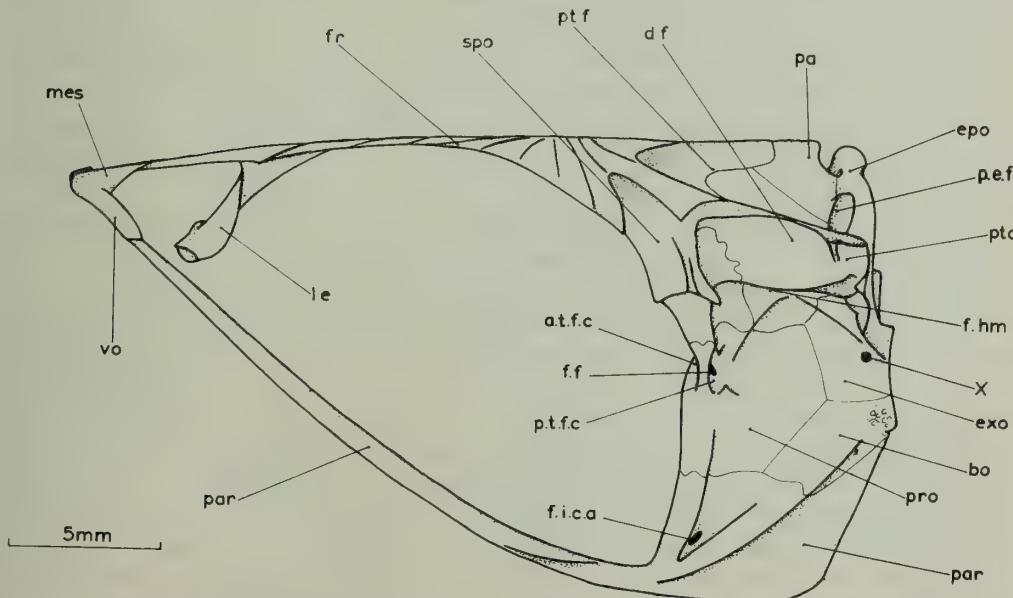


FIG. 34. *Enchodus lewesiensis* (Mantell). Neurocranium in lateral view.

with very slight expansions on either side, in the form of ventro-lateral flanges. The ventral surface has a shallow longitudinal groove, whereas the dorsal surface has a very low longitudinal ridge. Each ascending process of the parasphenoid meets the prootic laterally, and its anterior edge, bordering the myodome, is thickened. Posteriorly the ascending process is considerably thinner where it forms the wall of the myodome. In the antero-ventral region of the ascending process is a foramen through which the internal carotid artery passed. The posterior part of the parasphenoid articulates with the ventro-lateral edges of the basioccipital, and ends posteriorly immediately below the occipital condyle. The postero-ventral region of the parasphenoid takes the form of a median keel. This keel occludes a certain amount of the lumen of the posterior myodome and the myodome does not open posteriorly.

The prootic merits particular attention due to its complexity. The ventral part of the bone consists of two vertical laminae joined anteriorly. The inner sheet contacts the basioccipital behind and separates the myodome from the otolith chamber. The outer sheet forms the wall of the anterior part of the otolith chamber and meets the parasphenoid below and the basioccipital and exoccipital behind. The inner sheet curves medially and fuses with its partner from the opposite side forming the prootic bridge which separates the myodome from the cranial cavity. Posterior to the prootic bridge the otolith chambers communicate with the cranial cavity through a large oval fenestra. Above the prootic bridge the orbital face of the bone is roughly triangular, the apex of the triangle being directed ventrally. This region contacts the sphenotic dorso-laterally and the pleurosphenoid dorso-medially. Medially the edge of the prootic above the prootic bridge forms the margin of the lower part of the optic fenestra. The dorsal region of the lateral surface of the prootic is inclined dorso-laterally at about 110° to the ventral region. This upper region meets the exoccipital posteriorly, and the pterotic and sphenotic dorsally just below the hyomandibular facet. The prootic does not enter into the composition of the hyomandibular facet, which is produced solely from sphenotic and pterotic.

The prootic contains the trigemino-facialis chamber (Text-fig. 38A), which is divided by bone into a medial pars ganglionaris and a lateral pars jugularis. The former is a recess on the medial face of the bone, within the cranial cavity, lateral to the anterior part of the prootic bridge, and which housed the ganglia of the trigeminal and facial nerves. The pars jugularis is an extremely short horizontal canal on the lateral face of the prootic lateral to the prootic bridge, and in the angle between the dorsal and ventral parts of the lateral surface of the bone. There is a single foramen leading from the pars ganglionaris into the pars jugularis, this being the facial foramen which transmitted the hyomandibular trunk of the facial nerve. The palatine branch of the facial nerve did not enter the pars jugularis but passed through a small foramen medial to the facial foramen into the myodome. The pars jugularis has two external openings, one posterior and one anterior. Through this very short canal passed the jugular vein and the orbital artery. The posterior opening also transmitted the hyomandibular branch of the facial nerve. The

anterior opening of the canal is practically within the hind limit of the orbit. The remainder of the branches of the trigeminal and facial nerves did not enter the pars jugularis, but all passed through a single foramen in the hind wall of the orbit dorso-medial to the anterior opening of the pars jugularis. A notch occurs on the medial edge of the bone above the prootic bridge, this might indicate the course of the oculomotor nerve.

The pleurosphenoids, in the postero-dorsal region of the orbit, are separated in the mid-line by the large optic fenestra. Each bone meets the frontal dorsally and the prootic and sphenotic posteriorly. Beneath the frontals the bone is splayed apart and the superficial sheets of bone produced fail to contact the frontals medially. This area was in life presumably filled by cartilage.

The occipital condyle is circular and deeply concave. Ventrally it is formed of basioccipital. This single median bone passes forwards above the parasphenoid to meet the prootic anteriorly and the exoccipitals dorsally. In the angle between the condyle and the lateral region of the basioccipital there is a small group of pits and ridges. Internally the basioccipital forms the myodome roof and the floor to the otolith chamber. The basioccipital passes antero-dorsally to meet the prootics, separating the otolith chambers from the myodome. Dorsally the basioccipital bears a slight median crest which serves partially to separate the otolith chambers. The otolith chambers themselves extend anteriorly and end in a recess just posterior and ventral to the internal opening of the facial foramen.

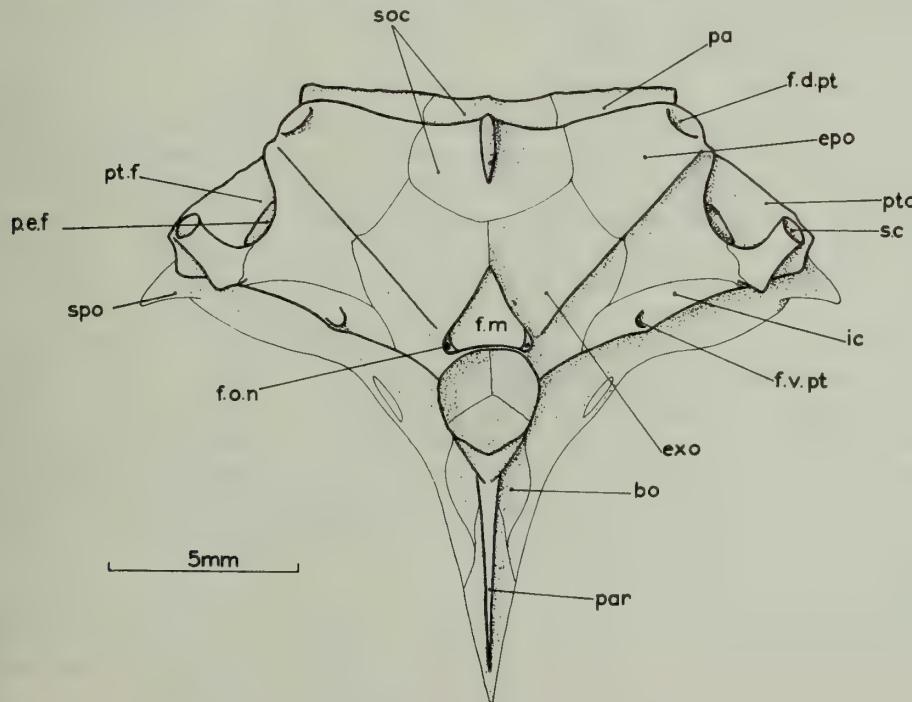


FIG. 35. *Enchodus lewisiensis* (Mantell). Neurocranium in posterior view.

The exoccipitals meet in the mid-line of the posterior face of the neurocranium both above and below the foramen magnum, completely enclosing it. Ventrally each exoccipital forms one dorso-lateral third of the occipital condyle. From the condylar region two struts of bone pass outwards, one laterally and one dorso-laterally; the lateral strut meets the pterotic, but this is overlain by the superficial intercalar. The ventral edge of this strut, near to the condyle, has a large foramen within it. This foramen transmitted the vagus nerve and possibly also the glossopharyngeal nerve. The dorso-lateral strut meets the epiotic and is continued upwards by the latter bone. Lateral to the foramen magnum the exoccipital is pierced by one or two very small foramina which appear to have transmitted occipital nerves. On the lateral face of the skull the exoccipital forms the postero-dorsal wall of the otolith chamber and meets the basioccipital ventrally, the prootic anteriorly, and the pterotic dorsally. Dorsally the exoccipital contributes to a large concave depression in the cranial wall which served to house musculature associated with the branchial apparatus. Internally, in the floor of the foramen magnum, the exoccipitals meet in the mid-line to form a shelf. The anterior edge of this shelf forms the posterior margin of the fenestra between the otolith chambers and the cranial cavity.

The intercalar is a moderately large bone incorporated into the cranial wall. It forms the main part of the lateral strut from the exoccipital and is wrapped around the postero-ventral corner of the braincase. It contacts the pterotic dorsally below the hind end of the hyomandibular facet. On the posterior face of the skull the intercalar bears a small projection which provided the articulatory region for the ventral limb of the post-temporal.

Hyopalatine bones. A reconstruction of the hyopalatine bones is shown in medial view in Text-figure 36. The hyomandibular is relatively deep and robust and is vertical in position. The head of the hyomandibular is single and elongate and fits into the grooved hyomandibular facet. The opercular process is situated about mid-way down the bone. Laterally the hyomandibular bears a shallow crest which runs obliquely back from the anterior region of the head of the bone. The anterior extent of the bone is considerably thinner and was covered in part by the metapterygoid.

The quadrate is large, stout and triangular. The condyle is ventral in position and is arranged transversely. The posterior region of the upper border bears a deep indentation which marks the upper margin of the groove on the medial face of the bone which housed the symplectic. The ventral region of the preoperculum rested against the posterior edge of the quadrate, which is considerably thickened. The anterior quadrate region is indistinct but it appears to be sandwiched between posterior extensions of the ectopterygoid, or both the ectopterygoid and the endopterygoid.

The ectopterygoid is bent through an angle of about 30° towards its posterior end where it overlaps the quadrate laterally. Both the ectopterygoid and endopterygoid are in the form of elongated laminae, which are fused along their ventral edges thus leaving a long dorsal V-shaped trough between them. The ectopterygoid is relatively shallow, the endopterygoid being much deeper. Anteriorly the ecto-

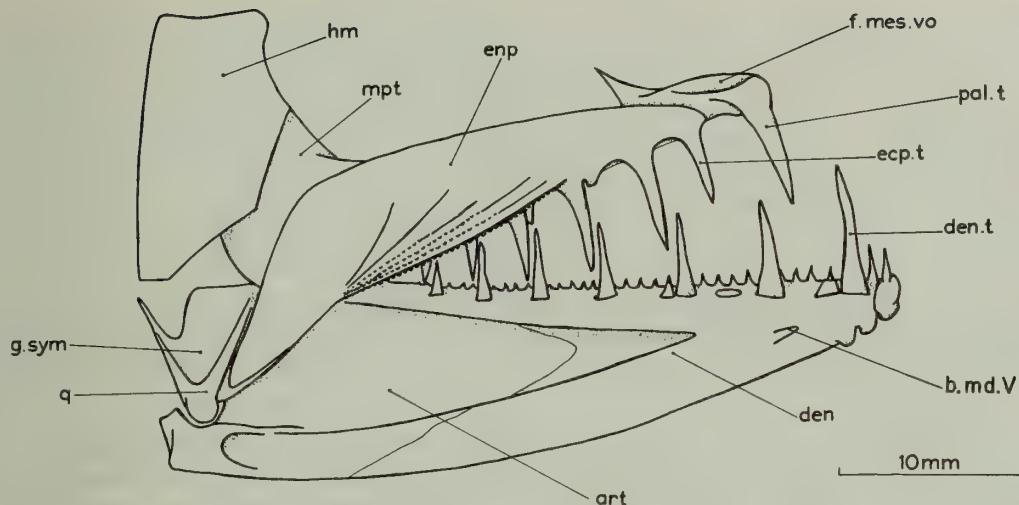


FIG. 36. *Enchodus lewisiensis* (Mantell). Hyopalatine bones and mandible of the left side in medial view.

pterygoid expands medially in front of the endopterygoid, so that both sides of the V-shaped trough are formed of ectopterygoid. The trough widens anteriorly into a U-shape, and the postero-ventral region of the palatine rests within it. On the ventro-lateral region of the palatine bone there is a longitudinal ridge projecting laterally and ventrally. The ectopterygoid spreads anteriorly, ventral to this ridge and articulates with its undersurface. Ventrally the ectopterygoid bears a row of large teeth which decrease in size posteriorly. The anteriomost ectopterygoid tooth arises from the ventral edge of the bone. Farther back along the ectopterygoid, the endopterygoid projects below the suture line between the two bones so that the more posterior teeth of the ectopterygoid series tend to arise from the ventro-lateral surface. The bases of the teeth are angled in such a manner as to make the main body of each tooth hang vertically downwards. There are approximately 7 functional teeth present on the ectopterygoid at any one time, and replacement teeth are visible close to the functional ones. All of the teeth are elongated and needle-like with well defined, but not particularly expanded bases. The teeth are laterally compressed to give rise to two cutting edges which are not strictly anterior and posterior, but set somewhat obliquely to the long axis of the ectopterygoid, and have a slightly recurved aspect.

The endopterygoid is visible from the lateral aspect as a small strip of bone below the region of fusion with the ectopterygoid. The endopterygoid bears a marginal row of minute teeth. On the internal face of the endopterygoid several more rows of minute teeth are seen radiating forwards and upwards. The more dorsal region of the endopterygoid inclines medially where it forms the roof of the mouth.

The palatines are characteristically shaped and composed of dense bone. The characteristic feature is the possession of a single, enlarged, terminal tooth. This

tooth is the longest tooth in the upper jaw and forms the continuation, anteriorly, of the tooth row on the ectopterygoid. The base of the tooth merges imperceptibly into the main body of the bone and is arranged at 90° to it. The tooth is, in all respects, identical to the pterygoid teeth, being laterally compressed to produce cutting edges. From its extreme anterior position and the fact that there is no other tooth base or any indication of a second tooth, it is assumed that this tooth is not replaceable and remained fully functional throughout life. On the dorso-medial region of the anterior end of the palatine there is a facet which housed the lateral wing of the mesethmoid and vomer. Posteriorly the palatine fits into the dorsal groove of the ectopterygoid and dorsally is extended to produce a facet for the reception of the ventral region of the lateral ethmoid. The lateral face of the palatine has a shallow, oblique, ill-defined groove in which the most anterior region of the maxilla was contained.

Dermal upper jaw. The dermal upper jaw consists of two bones, the maxilla and the premaxilla (Woodward, 1903, fig. 13). The premaxilla is particularly prominent with an anterior and a lateral region arranged at practically 90° to each other. There is an enlarged premaxillary pedicel anteriorly which contacts its opposite partner in the mid-line. The pedicels lie in the same plane as the anterior region of the skull-roof, and each pedicel contains a large oval foramen within it. The premaxillary pedicels articulate with the anterior edge of the mesethmoid. The lateral face of the bone is relatively smooth although grooves are present. One groove runs parallel with the pedicel at the anterior end of the lateral face, and a second very shallow groove runs along the oral border of the bone. The oral border itself bears a single row of marginal, acutely pointed teeth, approximately 20 in number.

The maxilla is long and slender, the head being unexpanded and incurved. The head of the maxilla rests in the groove on the lateral and dorso-lateral surfaces of the palatine. The maxilla slopes posteriorly and ventrally and was presumably attached to the premaxilla ligamentously. The maxilla is straight, of uniform shape, entering the gape of the mouth at the posterior end of the premaxilla. The maxilla shows no signs of having been provided with teeth.

Mandible. The mandible is shown in medial view in Text-figure 36. It is very long and deep, with the symphysial region much constricted and irregular in shape. The whole upper margin of the mandible is formed of dentary as well as the anterior two-thirds of the lower edge. The dentary is a large V-shaped bone with the apex toward the symphysis. The symphysis is deepened slightly by the presence of 2 or 3 small, finger-like ventral processes. Ventrally the bone is much thickened. The oral edge of the dentary gives rise to an internal tooth bearing flange. Anteriorly this flange contacts the lower thickened region demarcating an internal V-shaped space. This space presumably housed the remains of Meckel's cartilage. Teeth are present in two rows, a marginal row of minute, acutely pointed teeth approximately 30 in number; and an inner row of enormous teeth. These latter teeth are very similar to those found on the palato-pterygoid. The row consists of about 8 functional teeth. The anterior tooth of the series arises just behind the symphysis and is

considerably longer than the rest of the teeth although of the same form. The remainder of the teeth decrease in size posteriorly.

The articular forms the posterior mandibular region, and contains the concave, transversely orientated articular facet. There is a small retroarticular process behind the condyle which bears a deep groove passing around the condylar facet. This groove extends forwards ventro-laterally along the articular and dentary, and housed the mandibular sensory canal. The anterior and dorsal regions of the articular are in the form of a thin sheet of bone inserted on to the internal face of the dentary.

Ornamentation on the mandible is sparse ; a few longitudinal ridges occur at the ventral angle of the jaw radiating forwards and upwards on the articular. From the symphysial end of the dentary several ridges run backwards and downwards. The most prominent ridges are ventro-lateral in position.

ADDENDUM. A small very imperfect neurocranium from the English Chalk was also prepared in acid, B.M.N.H. number P.6461 (Text-figs. 37, 38B). This specimen had been noticed by Woodward (1901 : 193 and 1903 : 58) and included by him in the species *Enchodus lewesiensis*. This specimen would clearly seem to represent a species of *Enchodus* but there are several features which differ from those already noticed in the description of *Enchodus lewesiensis*. However since so little of the neurocranium is preserved and nothing of the remainder of the body, the erection of a new species is unnecessary. It will suffice here to point out the differences that are apparent.

Comparing the dorsal neurocranial views (Text-figs. 32 and 37), the differences in the relative proportions of the roofing bones are obvious. The actual cranial cavity is more elongated in P.6461 than in 4001 (the specimen used in the description of *Enchodus lewesiensis*). In fact the whole neurocranium would appear to have been longer and narrower in P.6461. The post-temporal fossae are similar in both specimens but the dilatator fossa of P.6461 is larger and clearly visible dorsally (as it is in *Enchodus faujasi* ; Goody, 1968, fig. 1). In 4001 the dilatator fossa faces laterally and is hardly visible from the dorsal aspect. The epiotic of P.6461 is more pronounced and backwardly projecting, and lateral to it, at the rear end of the post-temporal fossa, the fenestra entering the neurocranium below the fossa is larger than in 4001.

The most interesting difference between the two concerns the trigemino-facialis chamber in the prootic. This complex has been considered in some detail by Patterson (1964 : 434) where he deals with the changes that have occurred in the chamber during the evolution of the acanthopterygians. In P.6461 (Text-fig. 38B) the pars jugularis has three openings to the exterior. An anterior one in the hind face of the orbit, a posterior one opening on the lateral face of the prootic and a third one opening midway between the anterior and posterior openings. This last mentioned opening is large and the wall of the pars jugularis posterior to it is reduced to a narrow splint of bone. This opening would have transmitted the hyomandibular branch of the facial nerve dorsally, and presumably the orbital artery entered ventrally (the facial foramen leading into the pars ganglionaris in the medial wall of

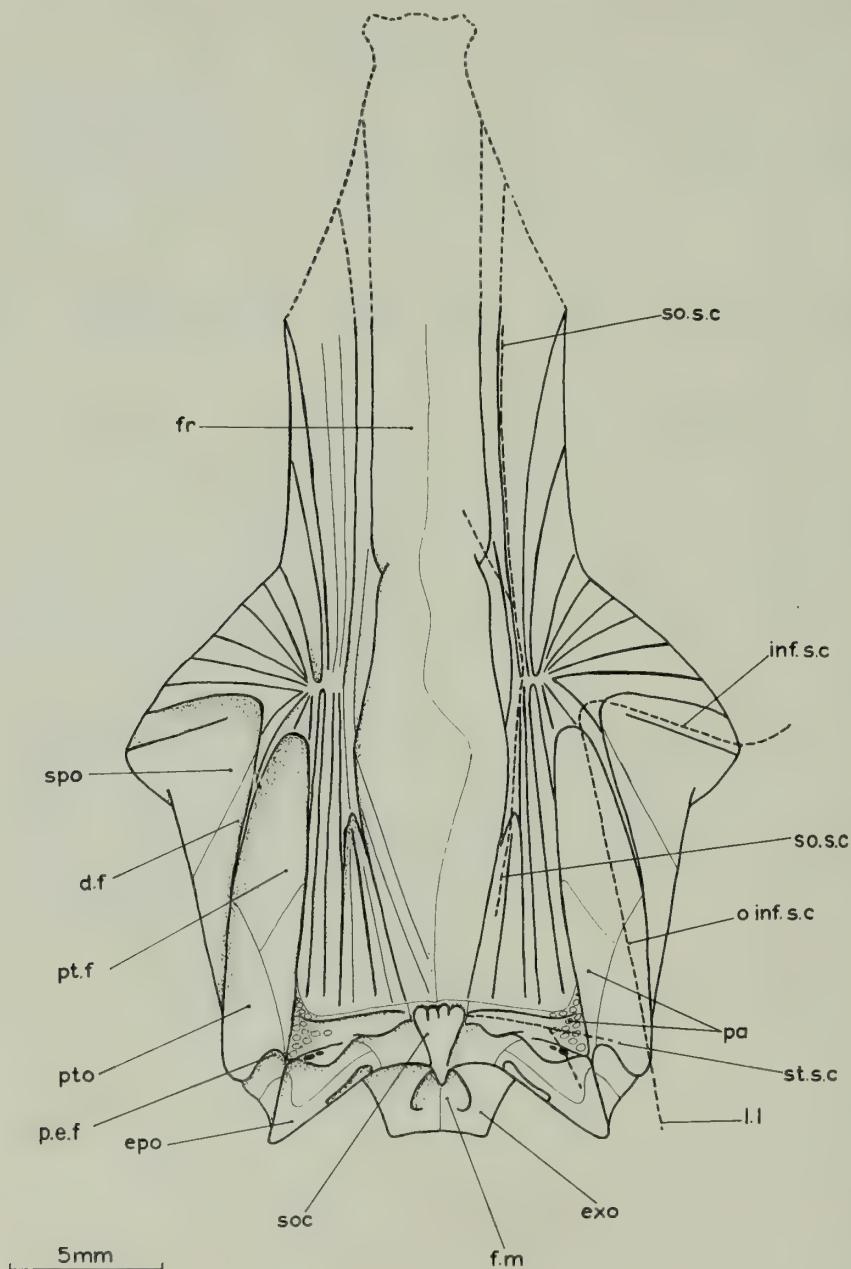


FIG. 37. *Enchodus* sp. Neurocranium in dorsal view. Only the restored outline of the anterior region is shown. The broken line on the right side of the figure indicates the course of the sensory canals. From B.M.N.H. number P.6461.

the pars jugularis is visible through this gap in the lateral wall). Vestiges of the narrow splint of bone forming the jugular canal are visible in 4001 (Text-fig. 38A) where they appear as small projections on the surface of the prootic both above and below the region of the jugular passage. The remainder of the trigemino-facialis chamber is similar in both specimens, with the trigeminal foramen opening into the hind wall of the orbit and not into the pars jugularis. In P.6461 a further small elongated foramen is seen dorso-medial to the trigeminal foramen and may have transmitted either the profundus or the oculomotor nerve.

If in fact specimen P.6461 does belong to the genus *Enchodus* then the degeneration of the wall of the jugular canal and the confluence of the hyomandibular and jugular openings can occur within a single genus. This process has been shown by Patterson (1964) to be a general trend within the teleosts associated with an overall advancement in bodily structure.

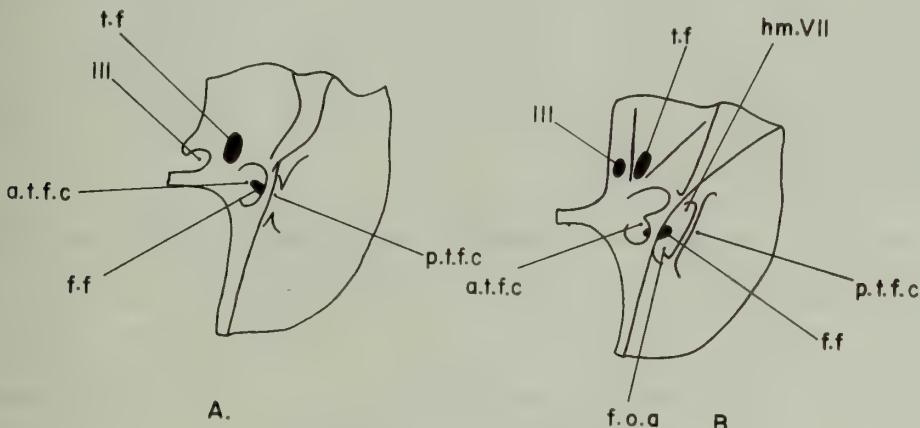


FIG. 38. Prootic bones in antero-lateral view. (A) *Enchodus lewesiensis* (Mantell). From B.M.N.H. number 4001. (B) *Enchodus* sp. From B.M.N.H. number P.6461.

Enchodus marchesettii (Kramberger)

(Text-figs. 39-42)

- 1895 *Eurygnathus marchesettii* Kramberger : 34, pl. 7, figs. 2, 2a.
- 1901 *Enchodus marchesettii* (Kramberger) Woodward : 200.
- 1903 *Enchodus marchesettii* (Kramberger) ; Hay : 421, pl. 30, figs. 2, 3.
- 1952 *Enchodus marchesettii* (Kramberger) ; Arambourg : 232, fig. 50.

DIAGNOSIS (emended). *Enchodus* species of standard length not exceeding 18 cm. The length of the head only just greater than the depth at the occiput, and just less than the maximum depth of the body. Head with opercular apparatus equal to one-third of the standard length. Mandible long and deep, its maximum depth being less than one-third of its total length. Teeth much smaller than in the type species. Maxilla thin and toothless. Operculum almost twice as deep as broad; suboperculum very deep. Dorsal fin consisting of 16 rays; anal fin with 20 rays and

arising behind the dorsal, nearer to the caudal than to the pelvics. Thirty-seven vertebrae of which 24 are caudal.

HOLOTYPE. Once in the Museo Civico di Storia Naturale, Trieste, present location unknown. The holotype was from the Middle Cenomanian of Hakel, Lebanon.

MATERIAL. Specimens in the B.M.N.H., numbers P.4748, P.9250, P.47316, from the Middle Cenomanian of Hakel and all prepared by the transfer method in acetic acid.

REMARKS. The species is known solely by flattened specimens from Hakel and Hajula in the Lebanon. Woodward (1901 : 200) noted this species and stated that it was not clearly distinguishable from *Enchodus longidens*. Hay (1903 : 421) separated *Enchodus marchesettii* as a distinct species. The neurocranium was not clearly observable in the specimens examined, but it does not appear to have differed to any noticeable extent from that of *Enchodus lewisiensis*, or that of *Enchodus faujasi* (Goody, 1968). Arambourg (1952 : 232, fig. 50) shows a photograph of the caudal skeleton and compares it with that of *Enchodus libycus* Quaas in which he indicates two large plate-like hypurals. This comparison of the two tail skeletons is open to some doubt when compared with the description and figure of the caudal skeleton presented below.

DESCRIPTION. *Neurocranium.* The frontals are visible merging anteriorly with the mesethmoid. Immediately posterior to this the lateral edge of the frontal bears a large elongated pore which is the anterior opening of the tube which in life contained the supraorbital sensory canal. The lateral region of the frontal is visible above the orbit and bears an ornamentation of tuberculated ridges. Above the sphenotic immediately posterior to the hind end of the orbit the postero-lateral region of the frontal is indented, indicating the anterior demarcation of the forward extent of the unroofed post-temporal fossa. This indentation is only in the upper ornamented layer of the frontal, since the frontal itself forms part of the floor of the anterior region of the fossa. The frontal overlaps part of the dorsal surface of the sphenotic.

The cranium is relatively deep in the posterior region but becomes shallower anteriorly. The orbit is very large, occupying about half the length of the neurocranium, while the cranial cavity itself is rather small. The frontal meets the parietal posteriorly in the medial wall of the post-temporal fossa. Immediately behind the parietal there is a rounded knob of bone which may have been separated partially from the parietal by a groove, this is the epiotic forming the occipital border of the skull-roof. The crest on the pterotic can be seen crushed slightly into the post-temporal fossa. This crest forms the lateral wall of the fossa, as well as the medial demarcation of the dilatator fossa. The suture between the sphenotic and pterotic is visible within the fossa. At the posterior end of the pterotic crest there is some evidence of a pore leading into a tube within the crest which transmitted the otic branch of the infraorbital sensory canal. The upper boundary of the hyomandibular facet, formed of pterotic and sphenotic, is visible below the dilatator fossa. The sphenotic forms the upper posterior limit of the orbit and extends

ventro-laterally. The parasphenoid is visible beneath the orbit as an almost straight rod of bone with no lateral expansions. From the underside of the frontals, above the orbit, the lateral ethmoid is produced downwards and connects with the hind end of the palatine. The frontals bear an ornamentation of prominent ridges, the major ridges running longitudinally, especially above the orbit, and following the course of the supraorbital sensory canal. The mid-region of the frontals is smooth and unornamented; some small ridges appear above the sphenotic and pass laterally to the upper margin of the orbit.

Infraorbital bones. The infraorbitals are shown in the lateral view of the skull, Text-figure 39. There are four narrow elongate infraorbitals and an elongated anterior lachrymal. The lachrymal is the largest bone in the series and is longer than deep. The antero-dorsal region of the lachrymal is produced dorsally, forming the anterior limit of the orbit. This dorsal projection articulates with the lateral ethmoid. Anteriorly and ventrally the lachrymal is expanded and overlaps the upper lateral region of the premaxilla. The ventral border of the lachrymal is slightly irregular in outline whilst the dorsal border is thickened and uniform. The infraorbital sensory canal was housed within a tube passing through each of the five bones which is incomplete in several places. On the lachrymal the sensory canal opened on to the surface of the bone in two places, anteriorly and antero-ventrally. The latter opening is in line with a groove on the lateral face of the premaxilla, which may have contained an anterior extension of the sensory canal. The lachrymal is thickened along the course of the sensory canal and shows some evidence

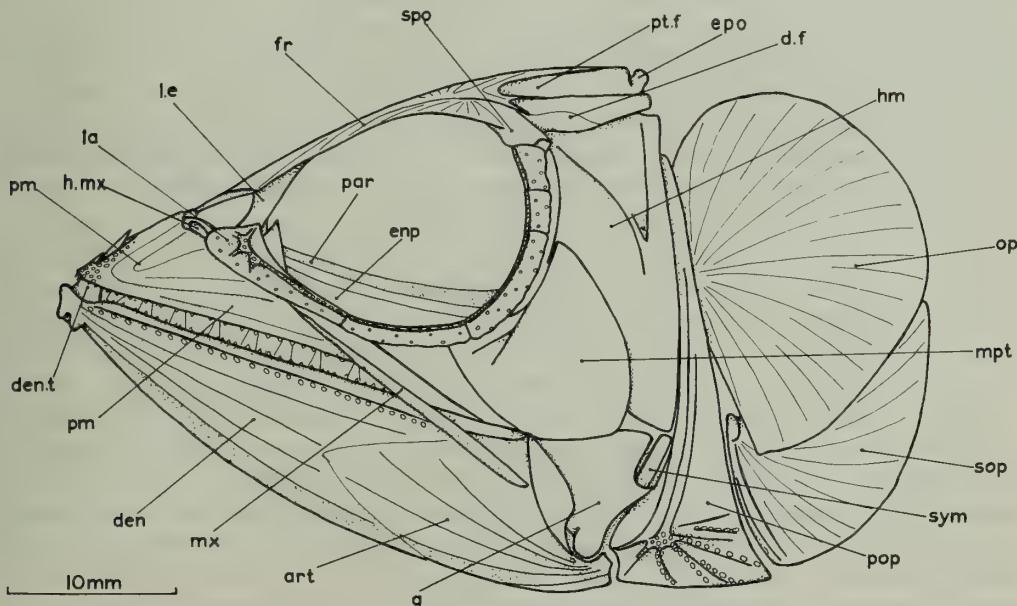


FIG. 39. *Enchodus marchesettii* (Kramberger). Restoration of the skull in lateral view.

postero-dorsally of the remains of a subocular shelf. The infraorbital bones decrease in length posteriorly, but not in width, none of the bones bearing any posterior expansion. The whole circumorbital series is ornamented with scattered tubercles which are most prominent above the course of the infraorbital sensory canal.

Hyopalatine bones. The general configuration of the hyopalatine bones is visible but the more detailed composition is masked by the covering of the dermal elements of the jaws, and by the rather poor state of preservation of the hyomandibular. The hyomandibular is large and deep with an antero-posteriorly elongated head. The posterior edge of the hyomandibular bears the condyle for the articulation of the operculum in its upper third. The lowermost two-thirds of the hyomandibular support the leading edge of the preoperculum. The lateral face of the hyomandibular is crossed by a crest which arises at the anterior region of the head and passes postero-ventrally in a curve to meet the rear margin about midway down.

The quadrate condyle is prominent and transversely orientated. Postero-dorsally the quadrate is indented, the posterior border of the excavation being lower than the remainder of the upper margin. This indentation marks the uppermost region of the recess on the medial face of the quadrate which housed the symplectic. The symplectic is present as a narrow rod of bone in B.M.N.H. number P.4748.

The pterygoid bones are indistinct. The ectopterygoid is a straight, laminate bone meeting the quadrate posteriorly and articulating with the palatine anteriorly. A single row of prominent teeth is present on the ectopterygoid. The endopterygoid can be seen within the orbit close to the parasphenoid where it forms part of the roof of the mouth. The metapterygoid is large, overlying the margin of the hyomandibular, but attaching ventrally to the dorsal edge of the quadrate.

The palatine is the characteristic tumid bone with an enlarged terminal fang at 90° to the axis of the bone. Posteriorly the palatine extends dorsally where it articulates with the lateral ethmoid internal to the lachrymal. Anteriorly the palatine is closely associated medially with the mesethmoid and vomerine regions. The head of the maxilla is just visible above the premaxilla, anterior to the lachrymal, lying in an oblique groove on the lateral face of the palatine. The terminal tooth is laterally compressed and bears fine longitudinal striations.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 39. It is composed of two bones, the premaxilla and the maxilla. The premaxilla is large and has two regions fused at 90° to each other. Anteriorly, lying in the same plane as the skull-roof, there are the premaxillary pedicels which meet each other in the mid-line and rest upon the anterior edge of the mesethmoid. Each pedicel contains an elongated oval fenestra within it. The remainder of the premaxilla is positioned laterally and is triangular in form, being drawn out antero-posteriorly. On the anterior region of the lateral face near to the pedicel there is a groove running parallel with the plane of the pedicel. This groove is in line with the anterior opening of the supraorbital sensory canal on the frontal. The premaxilla is overlapped dorsally by the ventral expansion of the lachrymal bone. Ornamentation in the form of scattered tubercles is present on the outer face of the premaxilla, the pedicel being more strongly ornamented than the rest of the bone. The premaxilla tapers

posteriorly and terminates just behind the end of the lachrymal, forming the anterior half of the oral margin of the upper jaw. There is a single marginal row of teeth which are small, acutely pointed and fused directly to the bone with no evidence of a tooth base. The teeth are evenly spaced and decrease in size posteriorly where they appear to be no more than an extension of the tubercular ornamentation.

The maxilla is an elongate, uniformly narrow strut of bone, entering the gape posteriorly. The head of the maxilla lies in a groove on the dorso-lateral surface of the palatine. The anterior region of the maxilla, behind the head, bears a small lateral flange under which the postero-dorsal edge of the premaxilla fitted. This flange tapers posteriorly to merge with the main shaft of the maxilla behind the premaxilla. The ornamentation of the maxilla is in the form of minute tubercles, which begin as two rows on the lateral flange and continue back as three rows along the remainder of the maxilla. The maxilla expands slightly towards its extreme posterior end and is laterally compressed where it rests against the lateral face of the mandible.

Mandible. The mandible is shown in lateral view in Text-figure 39. It is long and deep, but the depth is greatly reduced at the symphysis. The dentary is the largest component, forming the whole of the upper border, the anterior two-thirds of the lower border, and approximately half of the lateral face of the jaw. Internally the dentary gives rise to a tooth-bearing flange on the oral margin. This flange bears a single row of evenly spaced, relatively large, acutely pointed teeth, confined to the anterior two-thirds of the length of the jaw. The teeth are about 8 in number, laterally compressed, and decrease in size posteriorly. At the symphysis the anteriormost tooth is approximately twice as long as any of the other teeth in the row. Immediately in front of this tooth, at the extreme symphysial end, are two smaller teeth which are about one-quarter of the length of the longest tooth. All of the teeth are, however, identical in other respects. A second row of teeth is present on the extreme oral margin of the mandible, composed of between 30 and 40 small, pointed, laterally compressed teeth decreasing in size posteriorly.

The facet on the articular is deeply concave. The anterior edge of the facet is rolled upwards around the condyle, whilst posteriorly a short retroarticular process curves around behind the condyle. Postero-dorsally the articular is noticeably thickened. It joins the posterior end of the oral margin of the dentary to produce the coronoid process. The articular extends anteriorly to form the posterior region of the lateral face of the mandible.

The angular is a very small slip of bone on the postero-ventral angle of the jaw, below the articulatory facet.

The mandibular sensory canal ran along the ventro-lateral part of both the articular and the dentary. This canal entered the articular through a pore in the lateral face of the retroarticular process and passed within a tube of bone beneath the articular facet. Anteriorly the sensory canal continued forwards in a shallow groove in the dentary. The lateral face of the mandible is ornamented most markedly at either end of the jaw. The tubercles on the dentary radiate backwards from the symphysis, and on the articular forwards from below the facet.

Opercular bones. The opercular apparatus is shown in lateral view in Text-figure 39. The preoperculum is deep and narrow and curved somewhat forwards ventrally. It terminates dorsally below the head of the hyomandibular. The anterior edge of the preoperculum is thickened, this thickening is most pronounced in the ventral region, where the preoperculum abuts against the rear edge of the crest on the hyomandibular and the hind edge of the quadrate. The preoperculum widens ventrally and is produced into a short backwardly projecting spine. The preopercular sensory canal ran in a tube within the bone, opening dorsally by a single pore, and ventrally by three openings. Through the most anterior of these ventral openings the sensory canal passed into the mandible (B.M.N.H. number P.9250). The other ventral pores are directed more posteriorly. Laterally the preoperculum overlaps the anterior opercular region and bears an ornamentation of ridges and scattered tubercles, which are more pronounced on the ventral expanded area.

The operculum is large and deeper than it is long. The facet for the opercular condyle of the hyomandibular is in the upper half of the bone. The dorsal and posterior margin of the operculum is smoothly convex. From the opercular facet on the anterior edge a horizontal strengthening ridge crosses the internal face of the operculum, terminating on the posterior edge. The lateral face of the bone is ornamented with radiating rows of tubercles.

The suboperculum is large and deep, its dorsal part lying medial to the ventral part of the operculum. Antero-ventrally the bone is more robust and bears a

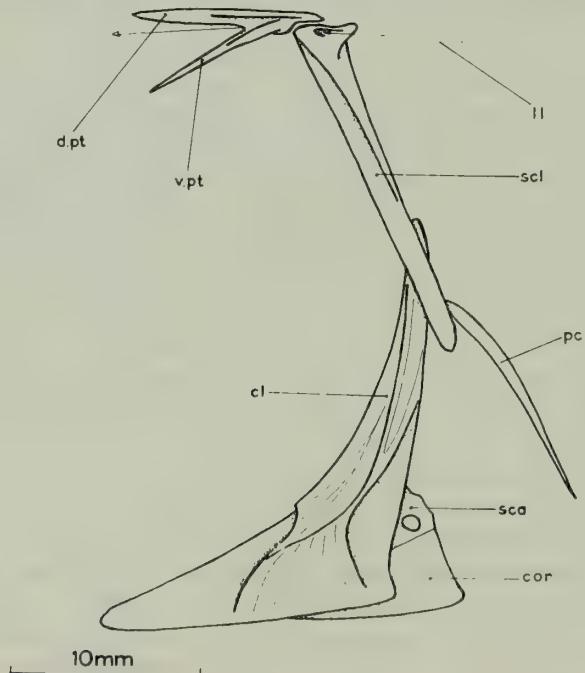


FIG. 40. *Enchodus marchesettii* (Kramberger). Pectoral girdle of the left side in lateral view.

vertical thickened rib on its anterior edge. Like the operculum, the suboperculum is ornamented with radiating tubercles. This radiation originates from a thickened knob at the antero-dorsal corner of the bone. The ornamentation is most pronounced ventrally and is absent where the bone lies medial to the operculum.

Pectoral girdle and fin. The pectoral girdle is shown in lateral view in Text-figure 40. The post-temporal has a flattened oval upper limb articulating with the epiotic. The dorsal surface of this upper limb is ornamented with tubercles radiating anteriorly and medially from a point on the postero-lateral region of the upper surface. The ventral limb of the post-temporal is approximately equal in length to the dorsal limb but is neither expanded nor flattened, simply being a narrow strut of bone articulating with the intercalar. Posteriorly the post-temporal is produced behind the junction of the dorsal and ventral limbs forming a facet into which the medial face of the head of the supracleithrum fitted. The lateral line canal entered the post-temporal bone through a postero-medial foramen in the anterior region of the supracleithral facet. It ran within a tube to open anteriorly in the angle between the upper and lower limbs of the post-temporal.

The supracleithrum is a long narrow bone with an expanded head housed in the medial facet of the post-temporal. The lateral line canal entered the head of the bone postero-laterally and left anteriorly within the post-temporal facet. The main shaft of the supracleithrum lies medial to the rear margin of the operculum. Ventrally it is attached to the lateral face of the upper extent of the cleithrum. The outer face of the bone is ornamented with a few longitudinal striations.

The cleithrum is large with a curved anterior border which is inclined medially to form the posterior limit of the branchial opening. The cleithrum narrows dorsally and ends medial to the ventral part of the supracleithrum. Ventrally the cleithrum is expanded laterally and terminates beneath the preoperculum. The expanded lateral region of the bone is ornamented with the characteristic tubercular ornamentation, while the more dorsal region is extensively ridged.

The endoskeletal girdle is masked by the lateral cleithral expansion. It does, however, project slightly, posterior to the cleithrum, where a scapula and coracoid are visible as well as a prominent scapular foramen. A saddle-shaped condyle on the rear edge of the scapula provided the articulatory point for the first fin ray.

The pectoral fin contains approximately 13 rays, all of which are segmented and branched distally except for the first ray which does not appear to be branched. A small postcleithrum is attached to the posterior edge of the ventral part of the supracleithrum.

Pelvic girdle and fin. The pelvic bone of either side is elongated, narrow and tapers to a point anteriorly, but is expanded posteriorly to produce the articulatory region for the pelvic fin rays. Medial to this articulatory region each pelvic bone bears a prominent horizontal flange which extends into the mid-line to contact its partner from the opposite side. The articulatory region consists of a projecting lateral condyle, supported by a prominent ridge. The rays of the pelvic fin are all segmented and branched distally except for the first ray which does not appear to

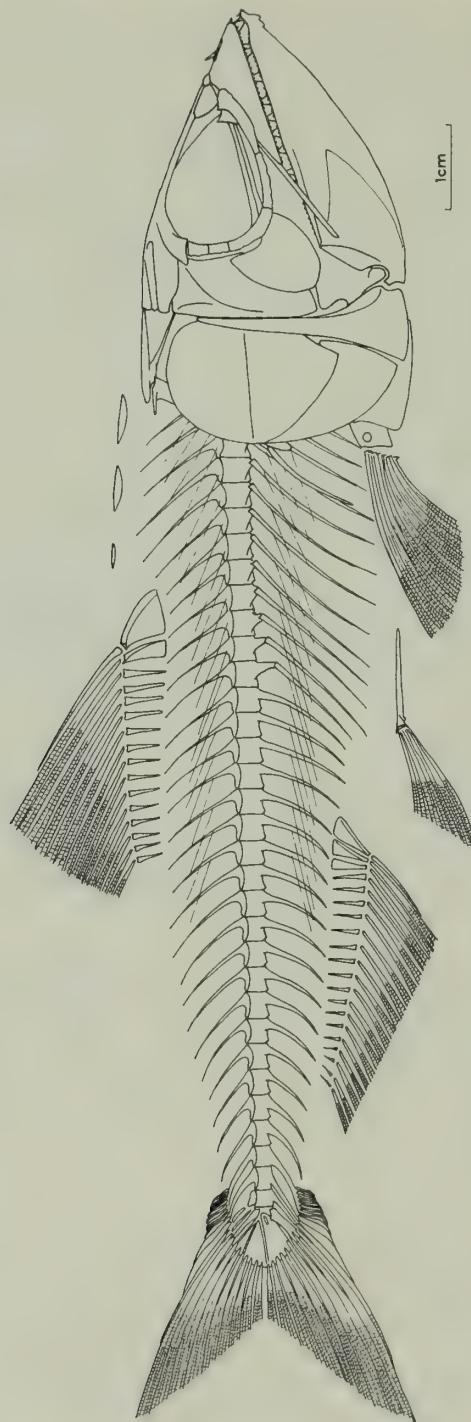


FIG. 41. *Enchodus marchesi* (Kramberger). Restoration of the skeleton, lateral line scales omitted but mid-dorsal scutes in position.

be branched. The number of rays contained in the fin is approximately 10. The position of the pelvic fins is abdominal, below the origin of the dorsal fin.

Vertebral column. The vertebral column is shown in the restoration in Text-figure 41. It consists of 37 vertebrae, of which 24 are caudal. The centra are slightly constricted mesially and are just longer than deep. The lateral face of each centrum bears a pronounced longitudinal ridge above and below which are prominent depressions. The neural arches occupy the entire length of the dorsal region of each centrum, and the neural spines emerge from the mid-dorsal region of each arch. The suture between the neural arches and the centra is always clearly visible. Anteriorly the neural arches have invariably become separated from the corresponding centra during fossilization indicating the looseness of this connection. More posteriorly the neural arches tend to be more closely attached to the centra. The precaudal vertebrae bear paired ventro-lateral transverse processes near the anterior end of each centrum. Pleural ribs articulate with these processes, the ribs themselves being long and flattened, and tapering to a point. The first two or three caudal vertebrae have a haemal arch with a gradually lengthening haemal spine, but also bear articulated pleural ribs of reduced dimensions. The subsequent haemal arches bear longer backwardly directed haemal spines.

Zygapophyses are present both above and below the column. The postzygapophyses are the more prominent dorsally, and the anterior zygapophyses are more prominent ventrally.

Epineurals and epipleurals are associated with the first 20 vertebrae.

Median fins and tail. The dorsal fin is positioned midway along the back and is composed of 16 rays, all segmented and all but the first branched. The first ray is shorter and stouter than the subsequent rays, the second is the longest. The rays decrease in size posteriorly. Each fin ray is supported by a pterygiophore, comprising an elongated proximal radial and a medial radial, the latter extending at a slightly oblique angle between the bases of adjacent fin rays. The distal radials are not distinguishable as separate elements, they are presumably incorporated into the fin ray bases. The more anterior proximal radials are expanded, especially the first which bears a large median keel projecting anteriorly.

The anal fin is composed of 20 rays and is confined to the more posterior part of the body. As in the dorsal fin the first ray is short and unbranched, as opposed to the longer, branched and segmented, subsequent rays. The radial composition is like that of the dorsal fin except that the most anterior proximal radial is unexpanded and the medial radials are less pronounced.

The caudal skeleton (Text-fig. 42) is composed of 6 vertebrae : three separate preural vertebrae (numbers 2, 3 and 4); a compound vertebra formed from the combination of preural vertebra 1 with ural vertebra 1; and a terminal half-centrum, the remains of ural vertebra 2. Preural vertebrae 3 and 4 bear slightly expanded, backwardly projecting neural and haemal spines which aid in the support of the accessory fin rays. The second preural vertebra (the first free preural vertebra) does not possess a neural spine, simply an expanded neural arch dorsally, and a markedly more expanded haemal spine ventrally. Preural vertebra 1 and ural

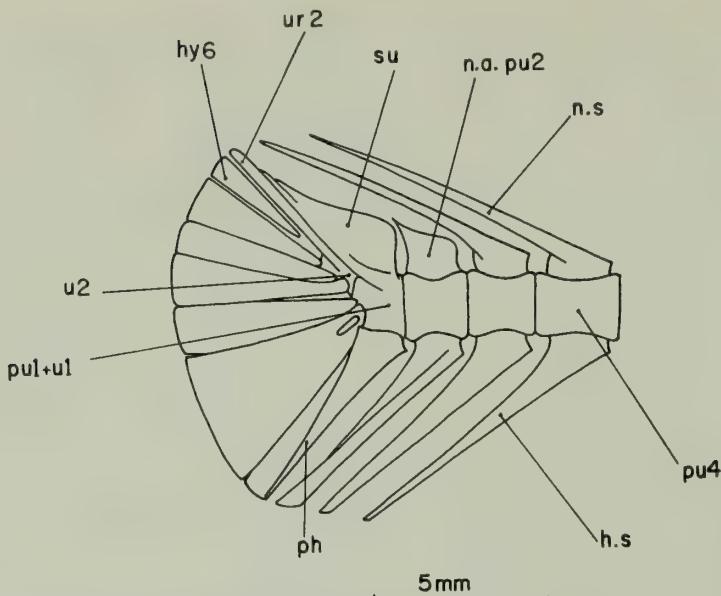


FIG. 42. *Enchodus marchesettii* (Kramberger). Caudal fin skeleton in lateral view.

vertebra 1 are fused with one another to produce a compound centrum which is slightly upturned. Articulating with this compound centrum are three structures, the parhypural, which represents the haemal spine of the first preural vertebra, and two hypural bones which extend up to the mid-line. The first hypural is the larger of the two, and basally bears a prominent fenestra. Dorsally the compound centrum bears an enlarged stegural element which projects postero-dorsally. The stegural bears an antero-dorsal expansion extending forwards towards the neural spine of the third preural vertebra. Posterior to the compound centrum ural vertebra 2 bears four hypurals, and may bear a second uroneural behind the postero-dorsal shaft of the stegural on the first ural vertebra.

The caudal fin consists of 19 principal rays, 17 of which are branched. There are 10 shorter accessory rays dorsally and ventrally in advance of the principal caudal rays.

Scales. The body is devoid of scales except for a row along the course of the lateral line and three reduced dermal scutes between the occiput and the dorsal fin. The line of scales marking the passage of the lateral line begins at the posterior region of the head of the supracleithrum, and extends along the whole length of the body, terminating on the lateral surface of the caudal peduncle. The row consists of 37 scales, the same number of scales as vertebrae, and each one is roughly rectangular in shape with its posterior margin deeply excavated. Each individual scale is very small and is isolated from its neighbours. The surface of each scale bears an ornamentation of small ridges and a backwardly directed spine which projects over the anterior region of the deep indentation. The spine is very small on the anterior

scales of the row but becomes progressively more pronounced posteriorly until, on the tail peduncle, it is an extremely prominent flange.

Genus ***PALAEOLYCUS*** von der Marck, 1863

DIAGNOSIS (emended) : Enchodontidae in which the body is elongated and no deeper than the depth of the head at the occiput. Vertebral number approximately 73 of which 40 are caudal. Pectoral fins greatly enlarged, pelvics excessively reduced. Anal fin greatly extended with 50 rays occupying one-third of the total body length, its origin being in advance of the dorsal fin. Dorsal fin itself much reduced in extent and positioned midway along the body. Mid-dorsal scutes not greatly reduced, 5 or 6 in number and almost overlapping.

TYPE SPECIES. *Palaeolycus dreginensis* von der Marck

Palaeolycus dreginensis von der Marck

(Text-fig. 43)

1863 *Palaeolycus dreginensis* von der Marck : 31, pl. 4, fig. 7.

1954 *Palaeolycus dreginensis* von der Marck ; Siegfried : 13, pl. 5, figs. 1, 2, 2a.
Siegfried lists earlier references.

DIAGNOSIS. As for genus, only species.

HOLOTYPE. Number 808 in the Paläontologisches Institut der Westfälische Wilhelms-Universität, Münster, from the Upper Senonian of Sendenhorst, Westphalia.

MATERIAL. The holotype and specimen number 8438, both from Sendenhorst and both in Münster.

REMARKS. Of the two specimens examined, the second specimen, number 8438, was the more complete and was the specimen used by von der Marck in his second work (1885 : 251). Neither specimen is complete by any means so that the following description is deficient in many features. No other specimens of the species are known to the author.

DESCRIPTION. *Neurocranium*. Little of the neurocranium is preserved, and what is observable is merely an impression in the matrix. The frontals appear to occupy a large proportion of the roof of the skull and are produced laterally as the upper border of the orbit. The sphenotic projects ventro-laterally from beneath the frontal at the hind end of the orbit and presumably the neurocranium attains its maximum width between the extremities of the sphenotics. The postero-lateral neurocranial region inclines ventrally and the presence of a vertical crest of bone is indicated in the pterotic region. The crest demarcates the dilatator fossa laterally and the post-temporal fossa medially, both fossae being unroofed. The neurocranial bones are unornamented except for the presence of raised ridges of bone running in a longitudinal direction above the orbit. The extent of the cranial cavity region is reduced, and is shorter than the diameter of the orbit which itself occupies at least

half the length of the neurocranium. The lateral ethmoid, at the anterior end of the orbit, is attached to the underside of the frontal, and ventrally is associated with a postero-dorsal expansion of the palatine. The frontal tapers anteriorly towards the mesethmoid region.

Jaws and suspensorium. The hyomandibular is large and vertical with part of its lateral face covered by the metapterygoid. The quadrate is large and triangular with a prominent transverse condyle at its ventral extremity. The ectopterygoid is an elongate laminar bone bearing a uniform row of teeth. The teeth are large, laterally compressed, just noticeably recurved, regularly spaced and decreasing in length towards the posterior end of the bone. The impression of a laminate endopterygoid is visible immediately below the orbit. The palatine is large and tumid and bears a single, enlarged terminal tooth set at 90° to the main body of the bone. Posteriorly the palatine is associated with the lateral ethmoid dorsally and the ectopterygoid ventrally. The palatine tooth is considerably larger than the teeth present on the ectopterygoid but in all other respects closely resembles them. The lateral face of the palatine bears traces of an obliquely inclined groove which may have housed the head of the maxilla.

The premaxilla appears large and irregularly triangular in outline. Impressions of the oral edge of the bone, between the anterior ectopterygoid tooth and the palatine tooth, show clearly that the premaxilla bore a row of small acutely pointed teeth. The premaxilla may occupy more than half of the oral border of the upper jaw with the maxilla entering the gape behind it. The maxilla is a stout, smooth, untoothed strut of bone.

The mandible is long and deep, its maximum length being almost four times its depth, and its minimum depth occurring at the symphysial end. The dentary forms the complete upper border of the jaw and well over half of the lateral face and the ventral margin. Teeth are present in a regularly spaced row with the anterior tooth at the symphysial end being greatly elongated. The jaws are closed in the specimens examined and the anterior dentary tooth lies against the anterior face of the palatine tooth and protrudes dorsal to it. The rest of the mandibular teeth are at most half as long as the anterior tooth and they decrease in size posteriorly. The articular bone forms the posterior end of the jaw and bears the articular facet for the reception of the condyle. The facet is rolled both anteriorly and posteriorly around the condyle and a small retroarticular process is produced posteriorly.

The preoperculum could not be observed in either of the specimens examined, although from the uprightness of the suspensorium it can be assumed that the preoperculum was vertical and relatively narrow. The operculum is large and considerably deeper than it is long. The facet for the articulation with the hyomandibular is positioned approximately midway along the straight anterior edge of the bone. The posterior edge of the operculum is smoothly rounded throughout. A horizontal strengthening ridge passes across the inner face of the bone from the articulatory facet to the posterior edge. The lateral face of the operculum is ornamented with a few weak ridges radiating from the region of the articulatory facet. A suboperculum is present but its limits are difficult to determine.

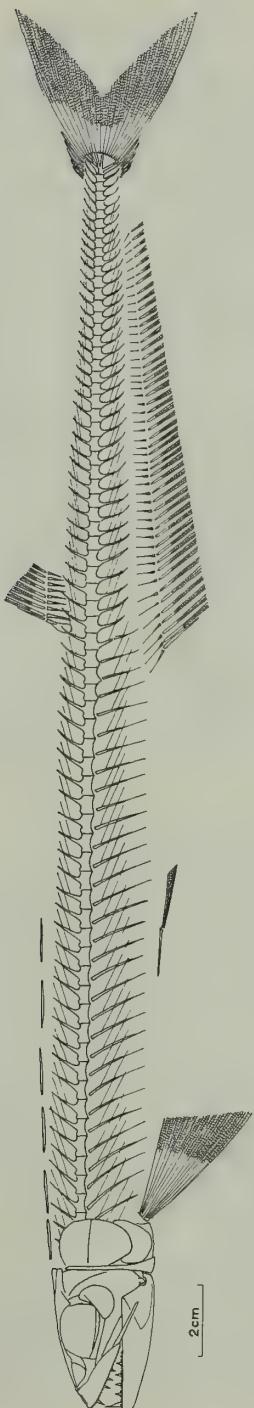


FIG. 43. *Palaeolycus dregenensis* von der Marck. Restoration of the skeleton, lateral line scales omitted but mid-dorsal scutes in position.

Paired fins, median fins and tail. A post-temporal bone of modest dimensions lies above the operculum, posterior to the occiput, and is composed of two limbs joined posteriorly. The dorsal limb is the more robust of the two. The supracleithrum is absent in both of the specimens and the cleithrum is also poorly preserved. The pectoral fin is enormous, arising well up on the flank while below its base a slight backward projection of the coracoid is visible. The fin consists of approximately 14 rays and is as long as, if not longer than, the entire length of the head (without the operculum).

The pelvic fin is much reduced and positioned about midway between the origin of the pectoral fin and the beginning of the anal fin. The exact number of pelvic fin rays could not be ascertained but it is obviously small. The rays themselves are very feeble.

The very small dorsal fin arises behind the origin of the anal fin, and appears to consist of 9 rays. The first ray is shorter than the subsequent ones and is unbranched. The second ray is the longest and the remainder decrease in length posteriorly. All of the fin rays are segmented and most, if not all, are branched.

The anal fin is greatly extended, its origin being a little over half way back along the body while it terminates close to the caudal fin. Forty-seven rays are visible in the fin, but there may possibly be a few more present (50). As in the dorsal fin the first ray is shorter than the rest and is unbranched.

The caudal fin is large, deeply cleft and consists of 19 principal rays, 17 of which are branched and segmented. Shorter, unbranched accessory rays are present both epaxially and hypaxially, there being 14 in all. The composition of the caudal skeleton was undeterminable.

Vertebral column. The body is considerably elongated and there appear to be 73 vertebrae, of which approximately 33 are precaudal. The individual centra are mesially constricted and longer than they are deep, although at the posterior end of the column the length of each centrum is reduced so that they present practically a square outline. Each centrum bears a neural arch and a neural spine, the latter arising from the middle of each of the neural arches. In the anterior precaudal region the neural spines are straight, but more posteriorly the spines show a marked backward curvature. The presence of a persistent notochord is shown by a continuous perforation throughout the length of each centrum. The precaudal vertebrae bear fine elongated pleural ribs which taper gradually to points. Haemal arches and spines characterize the caudal region, the arches arising from the anterior region of each centrum. Intermuscular bones, both epineurals dorsally and epi-pleurals ventrally, occur in continuous series along practically the entire length of the body.

Scales. The body is devoid of scales except for a row of dorsal scutes in the mid-line behind the occiput. There may be as many as 5 or 6 of these scutes and each one is ornamented with radiating bony ridges. No traces of lateral line scales were found in either specimen.

Family EURYPHOLIDAE nov.

DIAGNOSIS. Head not deepened and the body shallower than the greatest depth of the head which is at the occiput. Post-temporal fossa roofed. Lower jaw long and relatively shallow, the symphysis only slightly constricted. Articular facet not visible from the lateral aspect, being covered by a flange of bone laterally. Operculum as wide as deep with a posterior spine; the preoperculum also bears a prominent posterior spine ventrally. Pelvic fins as large as or larger than pectoral fins. Pectoral fins raised slightly on the flanks; pelvics sub-thoracic or abdominal in position. Cleithrum expanded posteriorly below the fin insertion. Lateral line scales overlap. Mid-dorsal scutes large and overlapping.

Genus **EURYPHOLIS** Pictet, 1850

DIAGNOSIS (emended). Eurypholidae in which the head is not particularly elongate and not shallow. Vertebral number between 35 and 40 of which the caudal region remains constant at 20 vertebrae. Body not lengthened or reduced in depth, maximum depth equaling the depth of the head at the occiput. Pelvic fins larger than the pectoral fins and sub-thoracic in position. Mid-dorsal scutes three in number and overlapping.

TYPE SPECIES. *Eurypholis boissieri* Pictet.

REMARKS. The genus *Eurypholis* is known by only two species, the type species and one other which was originally assigned to the genus *Enchodus* by Woodward (1901 : 193, *Enchodus pulchellus*).

***Eurypholis boissieri* Pictet**

(Text-figs. 44-48)

- 1850 *Eurypholis boissieri* Pictet : 30, pl. 4, figs. 2-4.
- 1866 *Eurypholis boissieri* Pictet ; Pictet & Humbert : 102, pls. 15, 16.
- 1887 *Eurypholis boissieri* Pictet ; Davis : 596.
- 1901 *Eurypholis boissieri* Pictet ; Woodward : 207, pl. 11, fig. 7, text-fig. 7.
- 1902 *Eurypholis boissieri* Pictet ; Woodward : 56, fig. 12.
- 1926 *Eurypholis boissieri* Pictet ; Woodward : 203, fig. 4.
- 1930 *Eurypholis boissieri* Pictet ; Maury : 96, pl. 1, fig. 2.
- 1932 *Eurypholis boissieri* Pictet ; Woodward : 160, fig. 247.
- 1940 *Eurypholis boissieri* Pictet ; Berg : fig. 143.
- 1958 *Eurypholis boissieri* Pictet ; Bertin & Arambourg : figs. 14, 16.
- 1964 *Eurypholis boissieri* Pictet ; Danil'chenko : 412, fig. 128.
- 1966 *Eurypholis boissieri* Pictet ; Lehman : 203, figs. 204, 205.

DIAGNOSIS (emended). *Eurypholis* of standard length not exceeding 10 cm. Head with opercular apparatus about twice as long as deep and occupying one-third of the standard length. Greatest depth of the mandible equal to one-sixth of the total length. Maxilla finely toothed. Dentary bearing two rows of teeth. Preoperculum deep, narrow and vertical. Operculum as deep as broad. Dorsal fin with 13 rays; anal fin with 14 rays arising behind the dorsal, nearer to the caudal peduncle than to the pelvic fin.

HOLOTYPE. Specimen number 639/58 in the Museum d'Histoire Naturelle, Geneva, from the Middle Cenomanian of Hakel, Lebanon, a head with the precaudal region.

MATERIAL. The holotype in Geneva and fifteen specimens in the B.M.N.H. The specimens used by Pictet (1850) and Pictet & Humbert (1866) were also examined in Geneva. All of the material examined was from the two Middle Cenomanian localities in the Lebanon, Hakel and Hajula.

REMARKS. All of the B.M.N.H. specimens were prepared in acetic acid by the transfer method. The only part of the skeleton which remains incompletely described is the neurocranium. All of the specimens of *Eurypholis* recovered from the Lebanese deposits are referable to the type species, being identical in body proportions and fin ray counts. The only variable feature in the osteology is the vertebral number, but this variation is within very narrow limits and the variability is confined to the precaudal region, the caudal region remaining constant at 20 vertebrae.

The references in the synonymy which occur after 1901 are simply mentions of the specific name together with the reproduction of Woodward's reconstruction of the body (1901 : text-fig. 7).

DESCRIPTION. *Neurocranium*. The neurocranium is shown in dorsal view in Text-figure 44. The cranial roof is flattened and widest at the hind border of the orbit between the sphenotics, and almost entirely composed of the frontals which extend back to near the occipital border. There is a straight suture between the frontals and a shallow median depression between the orbits which is more sparsely ornamented than the remainder of the skull-roof. The frontal extends on to the dorso-medial surface of the sphenotic, and the sphenotic just projects laterally from under it. The roof is covered by an ornamentation of raised bony tubercles radiating in all directions. Above the orbit and along the course of the supra-orbital sensory canal the tubercles are present on raised ridges of bone. Anteriorly the frontal tapers to end by insertion into (or under) the rear edge of the short, broad mesethmoid.

The supraoccipital is small, meeting the frontals anteriorly and separating the parietals laterally. In the mid-line the supraoccipital bears a small backwardly directed crest which does not extend dorsally above the plane of the skull-roof.

The parietals are transversally orientated, relatively narrow strips of bone bordered anteriorly by the frontals and laterally by the pterotics. Both the parietals and the supraoccipital are in part covered by the backward extension of the frontals. The tubercular ornamentation of the frontals is continued on the parietals and the supraoccipital. Near the posterior edge of the parietal a low transverse crest is present which functioned as an area for muscle insertion. The narrow strip of parietal and that portion of epiotic which is visible behind the crest are devoid of ornamentation.

The pterotic forms the postero-lateral border of the skull-roof, contacting the sphenotic anteriorly and the frontal and parietal medially. The dorsal surface of the pterotic is ornamented with tubercles which are connected by ridges of bone

giving an irregular latticed effect. This joining up of the tubercular ornamentation is visible to a certain extent on the postero-lateral region of each frontal.

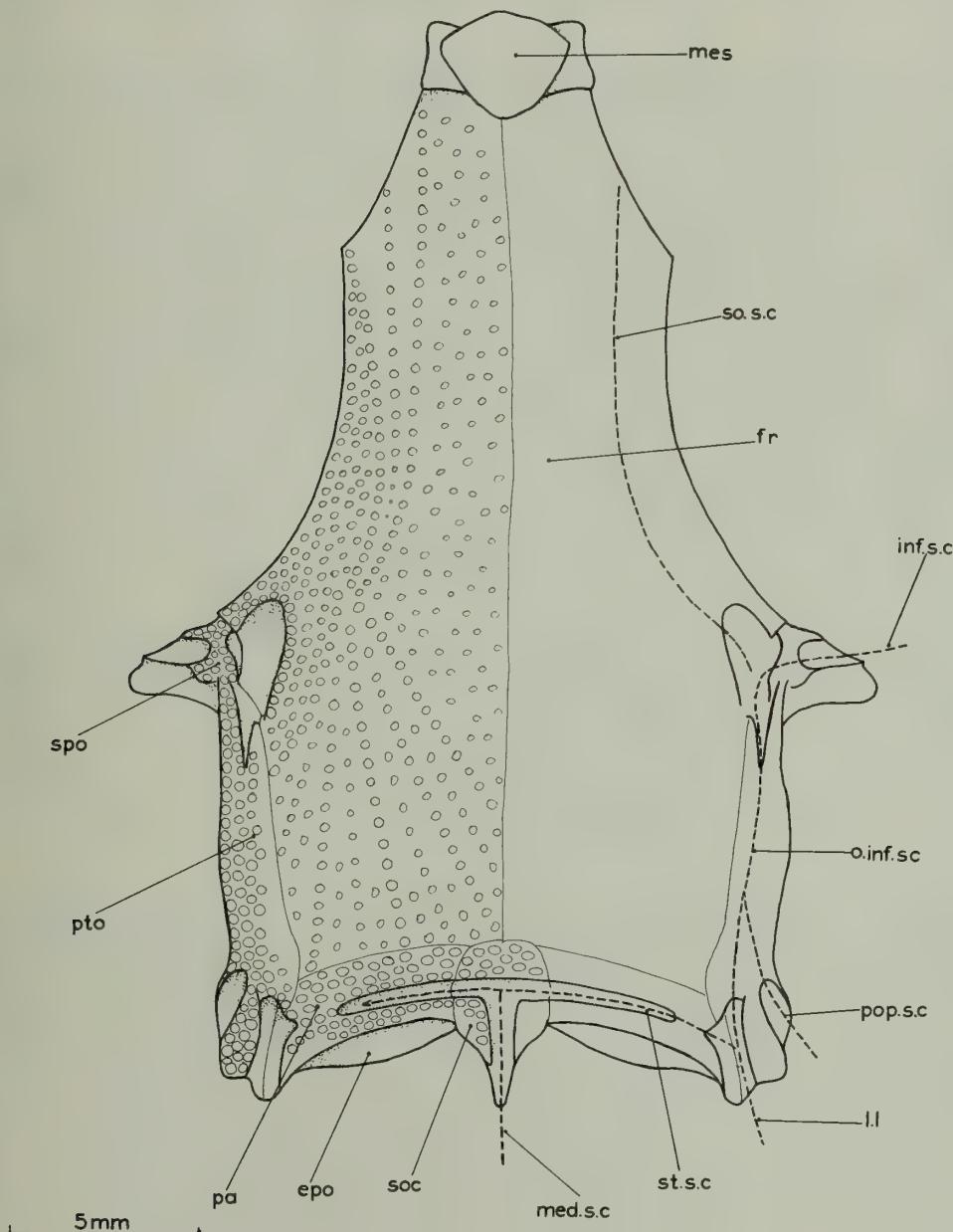


FIG. 44. *Eurypholis boissieri* Pictet. Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals.

The sphenotic forms the postero-lateral corner of the orbit, meeting the pterotic behind and the frontal medially. The dorsal surface of the sphenotic is in part ornamented with the latticed tubercular ornamentation already noticed on the pterotic.

The course of the sensory canals on the skull-roof is indicated by tubes within the bone and by grooves and depressions on the surface. The supraorbital sensory canal ran within a tube in the frontal opening anteriorly on the edge of the bone just posterior and lateral to the mesethmoid. Posteriorly this tube opens above the sphenotic in a triangular depression which is devoid of ornamentation. The main branch of the infraorbital sensory canal passed on to the dorsal surface of the sphenotic and entered a short tube within that bone which opens medially in the depression into which the supraorbital sensory canal passed. The otic branch of the infraorbital sensory canal entered the pterotic posteriorly through a pore at the anterior end of a short open groove. The sensory canal passed anteriorly within the pterotic and opened on to the dorsal surface of the sphenotic. Laterally, near the posterior end of the pterotic, a further foramen is present through which the preopercular sensory canal passed. A supratemporal canal was present running transversely across the skull-roof. This sensory canal connected with the otic branch of the infraorbital canal within the open groove on the posterior part of the pterotic. The canal passed medially in a tube within the parietal, but about midway along the bone the tube opens into a groove. This open groove is continuous across the dorsal surface of the supraoccipital from one parietal to the other. A further groove is seen in the mid-line of the supraoccipital connecting with and projecting back from the transverse groove. This groove seems to indicate that a further sensory canal was present in the mid-dorsal line of the body which connected with the supratemporal canal.

The mesethmoid is a short broad bone which is well ossified and closely attached to the dorsal surface of the vomer. The palatines articulate with the lateral wings of the mesethmoid, while the premaxillary pedicels are joined in the mid-line and articulate with the anterior edge of the mesethmoid.

Infraorbital bones. The infraorbitals are shown in lateral view in Text-figure 45. There are four infraorbitals and a large lachrymal in the circumorbital ring of bones. The bones decrease in size posteriorly and are unexpanded. Each bone in the ring carries a tube through which the infraorbital sensory canal ran. This tube opens occasionally on to the surface where it is simply a groove roofed by a flange of bone. The region of the sensory canal is ornamented with a single row of tubercles and the remainder of each infraorbital bone is sparsely tuberculated. The posterior bone of the series articulates with the sphenotic and received the sensory canal from the latter. The lachrymal is the anterior bone of the series and is longer than deep and dorsally bears a subocular shelf, but the remainder of the bones do not appear to exhibit this shelf. From the lachrymal an antero-dorsal projection articulates with the lateral ethmoid, while an anterior projection overlies the premaxilla laterally. The ventral border of the lachrymal is rounded and slightly roughened. The tube which contained the sensory canal runs within a dorsal ornamented thickened region,

and opens in two places on to the surface of the bone. One opening faces anteriorly, the other ventrally. The branch of the sensory canal which passed out through the anterior opening possibly continued on the lateral surface of the premaxilla where a distinct groove is observable.

Hyopalatine bones. The hyomandibular is large and has an elongated head. The lateral face bears a crest originating on the anterior region of the head and passing postero-ventrally to the rear of the bone where it is joined by a further crest running ventrally from the posterior region of the head. The combined crest passes ventrally, and shallows until it disappears at the ventral extremity of the bone. The opercular condyle is found on the posterior edge of the hyomandibular within the upper half of the bone. Laterally, anterior to the crest, the hyomandibular is thin and covered in part by the expanded metapterygoid. The quadrate condyle is normally not visible from the lateral aspect since it is covered by an upgrowth of the articular lateral to the articular facet. The quadrate is triangular in shape, and indented postero-dorsally at the upper limit of the groove on the medial face which contained the symplectic. The pterygoid region bears a uniform series of large, laterally compressed, acutely pointed teeth. The palatine bone is prominent and tumid and attached to the anterior end of the pterygoids. Postero-dorsally the palatine is slung from the lateral ethmoid and antero-medially it appears to be in association with the mesethmoid region. The palatine bears one enlarged terminal tooth which is set at 90° to the axis of the bone. This tooth is larger than those of the ectopterygoid but of similar form.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 45. It consists of two bones, the premaxilla and the maxilla. The premaxilla is large and in two main regions which are at an angle of 90° to each other. Anteriorly there is a premaxillary pedicel in the same plane as the skull-roof, containing an elongated fenestra. The pedicels meet in the mid-line and articulate with the anterior edge of the mesethmoid. The second region of the premaxilla is lateral in position and fuses with the lateral edge of the pedicel. In the region of fusion between the two parts of the premaxilla there is a deep groove passing anteriorly to the edge of the snout region. This groove is in a direct line with the anterior opening of the supraorbital sensory canal on the antero-lateral edge of the frontal. The postero-dorsal region of the premaxilla is overlapped laterally by the anterior region of the lachrymal. A ventro-lateral groove passing anteriorly to the edge of the snout possibly contained the most anterior region of the infraorbital sensory canal. The entire bone is ornamented with tubercles except in the mid-line on the pedicel. The premaxilla decreases in depth beneath the lachrymal and tapers posteriorly.

The maxilla enters the gape behind the premaxilla, the margins of both bones forming a continuous edge to the oral border. The maxilla is fused to the premaxilla and the line of demarcation is difficult to define. The maxilla has no ornamentation. The oral border bears a marginal row of teeth continuous with those on the premaxilla. The teeth are small, evenly spaced, acutely pointed and about 25 in number.

Mandible. The mandible is shown in lateral view in Text-figure 45. It is long and shallow, the depth being somewhat reduced in the symphysis region. The

UPPER CRETACEOUS TELEOSTS

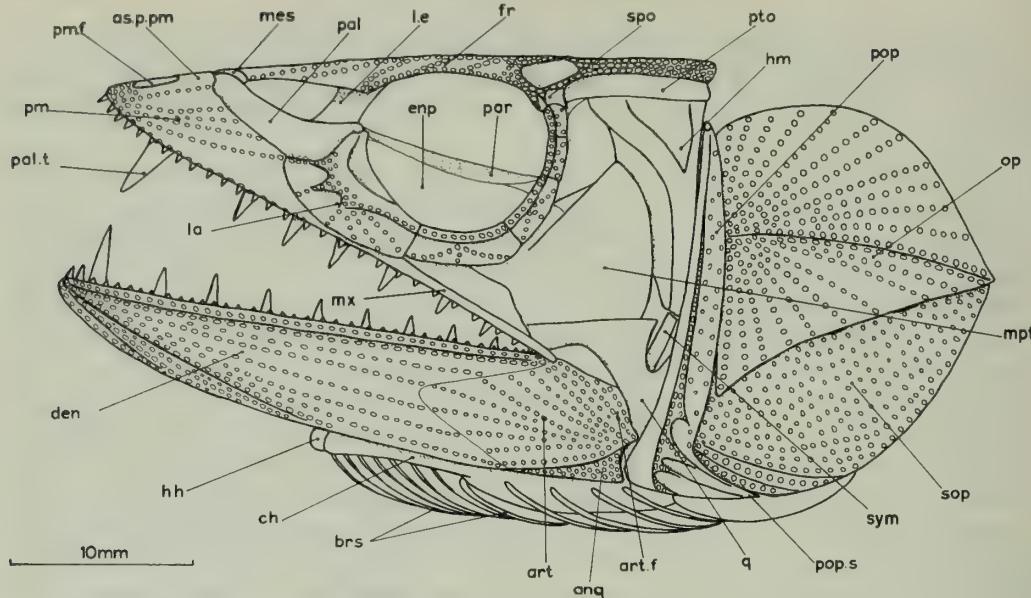


FIG. 45. *Eurypholis boissieri* Pictet. Restoration of the skull in lateral view.

dentary is the largest of the three bones and forms the complete upper border, the majority of the lower border and the anterior two-thirds of the lateral face. The posterior edge of the dentary is V-shaped. Internally the dentary gives rise to a tooth bearing flange on the oral margin which supports a single series of evenly spaced teeth, about 10 in number. The teeth are pointed, laterally compressed, slightly recurved, hollow and with expanded bases. The teeth are of approximately the same size except for the penultimate tooth at the symphyseal end of the mandible. This tooth is about twice the length of the other teeth in the row, but in all other respects closely resembles them. A second row of teeth on the oral margin of the mandible is composed of between 40 and 50 small, pointed, laterally compressed teeth which decrease in size backwards. In the posterior region these small teeth merge imperceptibly with the tubercular ornamentation on the lateral face of the mandible.

The articular facet is hidden from external view by a vertical upgrowth of bone from the lateral face of the articular. The articular forms, laterally, the posterior third of the mandible, occluding the V-shaped indentation of the dentary.

The angular is a small slip of bone forming the postero-ventral angle of the mandible beneath the articular facet. Its posterior face is slightly concave.

The mandibular sensory canal traversed both the articular and the dentary ventro-laterally. The lateral face of the mandible is ornamented with numerous tubercles, which are more prominent at the symphysis where they are raised on to ridges. The tubercles radiate in lines back from the symphysis on the dentary, and on the articular upwards and forwards from below the articular facet.

Opercular bones. The opercular bones are shown in lateral view in Text-figure 45. The preoperculum is deep and narrow and curved slightly forwards. It terminates

dorsally near to the uppermost region of the hyomandibular, and has a thickened anterior edge lying against the posterior edge of the hyomandibular crest. Ventrally the thickened edge of the preoperculum rests in a groove on the posterior thickened edge of the quadrate and is drawn out posteriorly into a prominent pointed spine. The preopercular sensory canal entered the bone through a dorsal pore and ran in a tube along the length of the bone, opening ventrally by two or three pores on or adjacent to the ventral spine. All of the visible openings are directed posteriorly, but the opening which transmitted the sensory canal to the mandible is usually hidden beneath the postero-dorsal upgrowth of the articular. The preoperculum is ornamented with the characteristic tubercles which are more prominent over the sensory canal. Posteriorly the preoperculum is thin and sparsely ornamented, although ventrally on the spine the tubercles are present on ridges of bone.

The operculum has a slightly concave anterior edge which abuts against the posterior face of the hyomandibular. Dorsally the operculum is rounded but ventrally and postero-ventrally the edge is slightly concave. From the opercular facet on the anterior edge a horizontal strengthening ridge is produced which crosses the internal face of the bone to terminate on the lower posterior angle where it is extended as a short spine. The lateral face of the operculum is ornamented with bony tubercles which radiate out from the point of articulation with the hyomandibular.

The suboperculum is large and dorsally lies internal to the ventral part of the operculum. Ventrally the suboperculum is more robust and bears tuberculated ridges, the dorsal region being more sparsely ornamented.

Branchiostegal rays. There appear to be 14 or 15 branchiostegal rays, the first 8 or 9 of which articulate with the ventro-lateral face of the ceratohyal, the tenth articulates with the region between the ceratohyal and epihyal, whilst the remaining 4 or 5 articulate with the lateral face of the epihyal. The anteriormost rays, on the ceratohyal, are smaller and thinner than the subsequent ones, which are broader based, more widely separated, and taper more rapidly. The terminal branchiostegal ray is the broadest of the whole series and arises on a level with the ventral region of the preoperculum, curving postero-dorsally along the ventral margin of the suboperculum.

Pectoral girdle and fin. The pectoral girdle is shown in lateral view in Text-figure 46. The post-temporal is horizontally arranged with an oval flattened upper limb articulating anteriorly with the epiotic. The dorsal surface of this upper limb is densely ornamented with raised bony tubercles. The ventral limb of the post-temporal is an elongated strut of bone, equal in length to the upper, which articulates antero-ventrally with the intercalar. The two limbs of the post-temporal join and the bone is produced posteriorly as a small vertical flange. A postero-medial facet is found on this flange and the facet contained the anterior region of the head of the supracleithrum. The lateral line canal passed within a tube through the bone. The anterior opening of the tube is clearly shown on the lateral face of the post-temporal.

The supracleithrum is long and narrow, with an antero-posteriorly elongated head. The lateral line canal passed straight through the head of the supracleithrum within a tube. Ventrally the supracleithrum lies against the upper lateral face of the cleithrum, and here the supracleithrum bears several vertical striations on its lateral face.

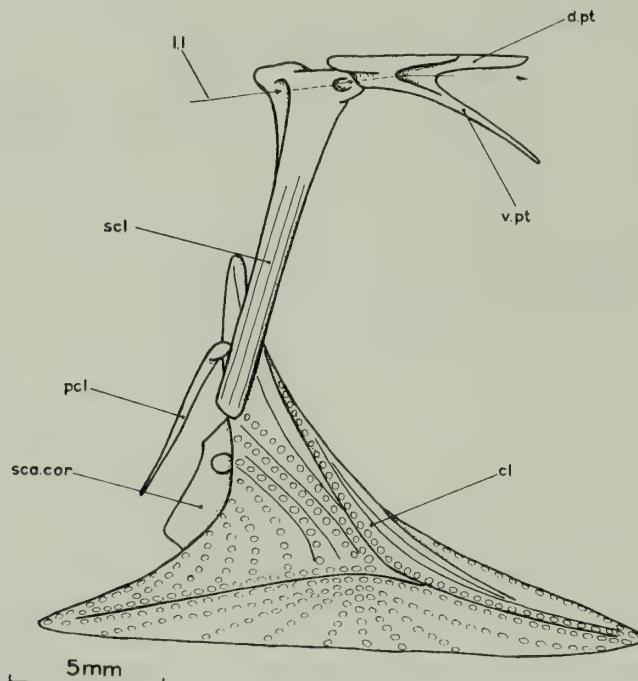


FIG. 46. *Eurypholis boissieri* Pictet. Pectoral girdle of the right side in lateral view.

The cleithrum (post-clavicular plate of Woodward, 1901 : 208, fig. 7) is a very large and characteristically shaped bone. The anterior margin is inclined medially where it forms the posterior boundary of the branchial opening, and the lateral face is greatly expanded both anteriorly and posteriorly, particularly in the ventral region. The anterior termination of the cleithrum lies medial to the extreme ventral end of the preoperculum, and the posterior end of the cleithrum extends for a considerable distance backwards below the pectoral fin. Both of these extremities are acutely pointed. The ventral region of the cleithrum, as well as being expanded anteriorly and posteriorly, is also inflected strongly towards the mid-ventral line of the body, approaching its partner from the opposite side. The whole external face of the cleithrum is ornamented with the characteristic tubercles, which are most prominent near the anterior and the ventral edges. Dorsally the cleithrum tapers and lies medial to the supracleithrum.

The endoskeletal girdle attaches to the internal face of the cleithrum, but owing to the great expansion of the cleithrum its outlines are not determinable: a large

scapular foramen is, however, visible. Four small hour-glass shaped radial bones are present on the posterior edge of the scapulocoracoid and with these the 13 rays of the pectoral fin articulated. The first ray is the longest, the rest gradually decreasing in size. Due to the posterior expansion of the cleithrum, the pectoral fin is raised slightly so that its point of insertion has moved up the flank.

A small, narrow and curved postcleithral bone attaches to the postero-ventral part of the supracleithrum and projects postero-ventrally, lying medial to the radial elements of the pectoral fin.

Pelvic girdle and fin. Each pelvic bone is composed of a roughly triangular sheet of thin bone which is flattened and meets its partner in the mid-ventral line just posterior to the cleithrum. The pelvic bones therefore can be said to be sub-thoracic in position. Each bone bears a thickened condylar region posteriorly which lies lateral to an articulatory facet. The condyle is supported by a ridge passing anteriorly along the lateral edge of the bone. The pelvic fin consists of 8 stout rays all of which are branched distally and segmented.

Median fins and tail. The median fins are shown in the restoration, Text-figure 47. The dorsal fin is somewhat deeper than long and contains 12 rays. The first ray is shorter than the subsequent ones and segmented but not branched. The elongated proximal radials are prominent and all are expanded to a certain extent, especially the first which bears a large median keel projecting anteriorly. The distal ends of the proximal radials are expanded at the bases of the fin rays and the medial radials extend obliquely between the bases of adjacent fin rays.

The anal fin consists of 13 or 14 rays. The first ray is shorter than the second and is unbranched : the remainder are all branched. All the rays are segmented. The pterygiophore composition of the anal fin parallels that of the dorsal fin except that the proximal radial at the anterior end is not expanded.

There are six vertebrae entering into the composition of the caudal skeleton (Text-fig. 48), three free preural vertebrae, one free ural vertebra, and a compound vertebra formed from the fusion of the first preural vertebra and the first ural vertebra. Preural vertebrae 3 and 4 both bear normal neural spines, which are strongly inclined posteriorly, and ventrally these preurals bear expanded haemal spines. Preural vertebra 2 (the first free preural vertebra), bears a greatly expanded haemal spine ventrally but does not possess a neural spine, simply an enlarged neural arch. The compound vertebra formed from the fusion of preural vertebra 1 with ural vertebra 1 bears a parhypural ventrally (the haemal spine of the first preural vertebra), and two hypurals which extend dorsally to the mid-line. The ventral-most hypural (hypural 1) is by far the larger of the two and has an oval foramen near to its base. Dorsally the compound centrum bears an expanded stegural which extends as a rod-like structure in a postero-dorsal direction, and has a thin anterior projection in the mid-line which extends forwards towards the neural arch of preural vertebra 2. The second ural vertebra is in the form of a small half-centrum which bears a posterior fan of four hypurals supporting the upper lobe of the caudal fin. The second ural vertebra also appears to bear a second uroneural element closely associated with the posterior edge of the stegural. At least one

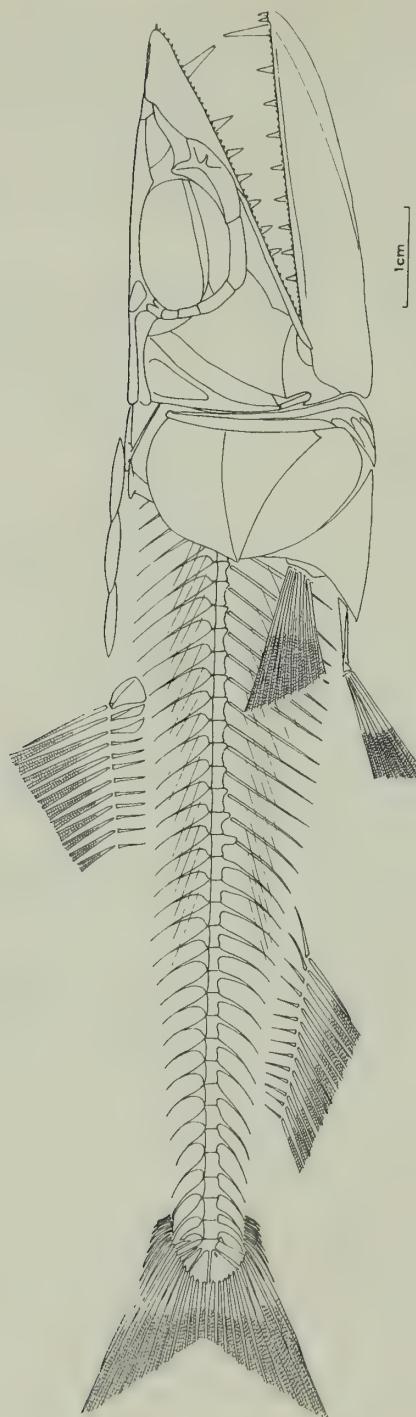


FIG. 47. *Eurypholis boissieri* Pictet. Restoration of the skeleton, lateral line scales omitted but mid-dorsal scutes in position.

epural is present anterior to the postero-dorsal extension of the stegural. The number of principal rays is 19 of which 17 are branched. There are at least 10 accessory rays epaxially and 10 hypaxially.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 47. In the specimens examined the vertebral number ranges from 35 to 40, and the centra are constricted. Of the total number of vertebrae approximately 18 are precaudal, the remainder (approximately 20) are caudal. The lateral face of each centrum bears a pair of longitudinal ridges between which is a rectangular depression. The neural arches occupy the entire dorsal surface of each centrum with the neural spines arising near to the posterior end of each arch. The suture between the neural arch and the corresponding centrum is clearly visible and the most anterior neural arches have a tendency to be separated from the centra during fossilization. Prezygapophyses and postzygapophyses are present on the neural arches but neither are particularly prominent.

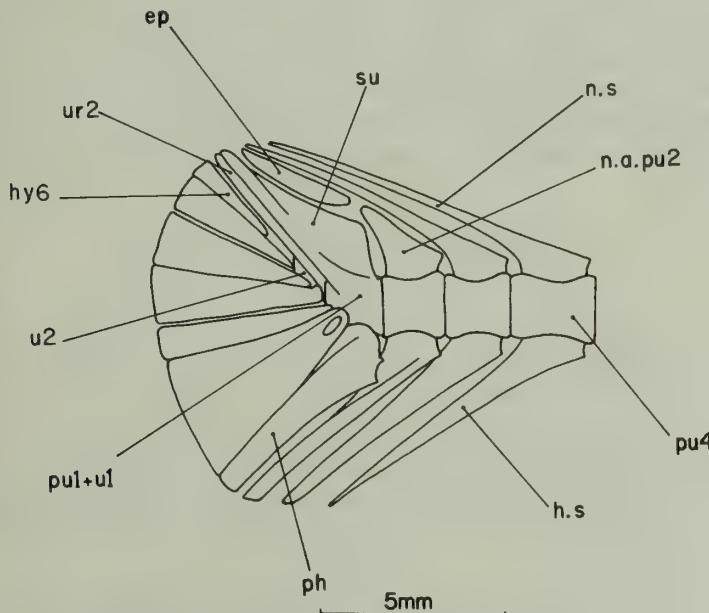


FIG. 48. *Eurypholis boissieri* Pictet. Caudal fin skeleton in lateral view.

The precaudal vertebrae bear paired ventro-lateral transverse processes on the anterior end of each centrum. Pleural ribs articulate with these parapophyses, and the ribs are moderately long and flattened. The ribs decrease in size posteriorly. All of the haemal arches, except for the first, are drawn out posteriorly into haemal spines. Epineurals and epipleurals are associated with the first 30 vertebrae.

Scales. The body is devoid of scales except for a row along the course of the lateral line, and three large dermal scutes between the occiput and the dorsal fin in the mid-dorsal line of the body. These dorsal scutes are oval in shape and bear

median longitudinal ridges on their dorsal surfaces. Each scute is ornamented dorsally with concentric ovals of small raised tubercles. The scutes overlap slightly and extend almost back to the origin of the dorsal fin. These scutes definitely give the appearance of having had a sensory canal associated with them, particularly as there is evidence of a median dorsal sensory canal which passed on to the supraoccipital and may possibly have passed through these three dorsal scutes.

The scales marking the passage of the lateral line canal begin just posterior to the dorsal supracleithral region and continue back along the length of the body to terminate on the caudal peduncle. There are approximately the same number of scales in the row as there are vertebrae, i.e. 40. The scales are irregularly triangular, the base of each triangle being directed posteriorly. Each scale has a single deep indentation posteriorly, and here it overlaps the anterior region of the next scale in the row. On the anterior region of each scale there is a raised median ridge which is continued as a projection posteriorly above the anterior region of the hind indentation. The outer surface of each scale is ornamented with small scattered tubercles except in the anterior region which is overlapped by the preceding scale. The individual scales were perforated by the sensory canal which also ran within the posterior indentation of each scale. The projecting spine on each scale becomes more pronounced near the posterior end of the body, especially on the caudal peduncle where the terminal two or three scales bear prominent laterally projecting flanges.

Eurypholis pulchellus (Woodward)

(Text-figs. 49-54)

1888a *Enchodus lewesiensis* (Mantell) ; Woodward : 315, pl. 1, fig. 6 (*errore*).

1901 *Enchodus pulchellus* Woodward : 193, pl. 11, figs. 2, 3.

1903 *Enchodus pulchellus* Woodward ; Woodward : 62, pl. 14, figs. 9-11, text-fig. 14.

DIAGNOSIS (emended). *Eurypholis* in which the maxilla does not appear to be toothed. A single major tooth row on the dentary with no indications of a marginal row. Mandible long and narrow with its greatest depth being about one-fifth of the total length. Preoperculum deep and narrow and forwardly inclined. Operculum slightly deeper than broad.

HOLOTYPE. Specimen number P.1703 in the B.M.N.H., an isolated head exposed from the left side, from the Turonian of south-east England.

MATERIAL. The holotype and one other specimen from the B.M.N.H., number P.10984, also from the Turonian of south-east England.

REMARKS. This species was originally placed by Woodward in the genus *Enchodus*. At first (1888a : 315, pl. 1, fig. 6) Woodward included it in the species *Enchodus lewesiensis*, later however he erected a new species for its reception, *E. pulchellus* Woodward (1901 : 193). The holotype figured by Woodward (1901, pl. 11, fig. 2 ; and 1903, pl. 14, fig. 9) is the remains of a head on a block of chalk with the left side exposed. The specimen was mechanically prepared from the right side, thus exposing much of the neurocranium and showing it to be unlike the neuro-

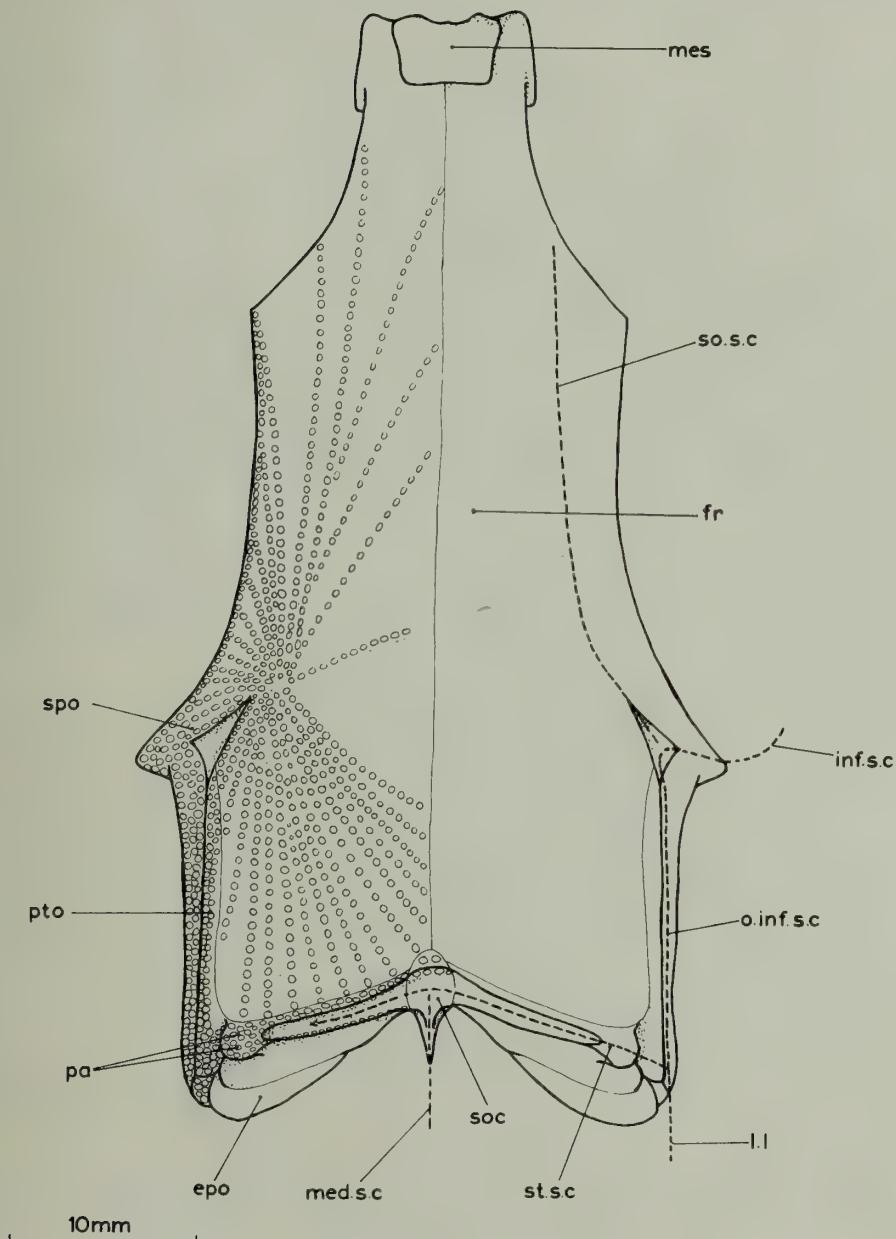


FIG. 49. *Eurypholis pulchellus* (Woodward). Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals. From B.M.N.H. number P.1703.

cranium of *Enchodus lewesiensis*. Apart from the size difference the cranial roof is practically identical to that of *Eurypholis boissieri*. In order to elucidate these points a second specimen was prepared in acid, P.10984, from the *Holaster sub-globosus* zone of Hitchin, Hertfordshire. This, like the holotype, was exposed from the right side. The neurocranium which was recovered after acid treatment was incomplete only in respect of the roof region. Thus using the two specimens P.1703 and P.10984 a complete description of the neurocranium and jaws was obtained. Although the body is missing from both specimens, the head supplies ample justification for transferring the species to the genus *Eurypholis*.

DESCRIPTION. *Neurocranium.* The neurocranium is shown in dorsal, ventral, lateral and posterior views in Text-figures 49–52. The cranial roof is flattened and attains its widest point behind the orbits in the sphenotic region. The frontals cover practically the whole of the skull-roof and meet in the mid-dorsal line in a straight suture. The interorbital region of the skull-roof is slightly depressed and more sparsely ornamented. The frontal contacts the dorsal surface of the sphenotic and spreads partially above it. The entire roof is covered by an ornamentation of raised tubercles, and where the sensory canals passed within the bone the ornamentation is accentuated, the tubercles being raised on bony ridges. The ornamentation radiates outwards from the centre of ossification. Anteriorly the frontals taper from in front of the orbits and are inserted into the rear edge of the mesethmoid. Postero-laterally the frontal contacts the pterotic, and posteriorly the parietal and the supraoccipital.

The supraoccipital is a small median bone contacting the frontals anteriorly and separating the parietals. In the mid-line of the posterior face of the supraoccipital is a small backwardly directed crest.

The parietals are narrow, transversely elongated strips of bone. Anteriorly the parietals are bordered by the frontals and posteriorly by the epiotics. The tubercular ornamentation of the frontal bone is continued on to the parietal and the supraoccipital. A shallow groove present on each parietal bone is continuous with a shallow transverse groove on the supraoccipital. Behind the transverse groove on the parietal the hind border of the skull-roof is composed of a further strip of the parietal bounded posteriorly by the epiotic. This posterior part of the parietal is unornamented, probably indicating that the epaxial musculature encroached on to the postero-dorsal surface of the skull-roof.

The pterotic forms the postero-lateral border of the skull-roof, joining the sphenotic anteriorly, the frontal and parietal medially, and the epiotic posteriorly. The dorsal surface of the pterotic is heavily ornamented, the tubercles being joined by intervening ridges of bone to give an irregular latticed appearance.

The sphenotic forms the postero-dorsal region of the orbit and contacts both the frontal and the pterotic. The dorso-medial region of the bone is ornamented similarly to the pterotic, but more laterally the surface becomes smoother.

The course of the sensory canals on the skull-roof is indicated by tubes within the bone and open grooves on the surface. The supraorbital sensory canal passed forwards within the frontal and emerged anteriorly on the lateral edge of the frontal.

Posteriorly this tube opens above the sphenotic into a shallow triangular depression devoid of ornamentation. The infraorbital sensory canal crossed the dorso-lateral surface of the sphenotic before it entered the bone. It opened again more medially into the triangular depression already noticed in association with the supraorbital sensory canal. The otic branch of the infraorbital sensory canal entered the pterotic posteriorly and passed forwards within the bone also to open anteriorly into the triangular depression. A postero-lateral pore is visible in the pterotic and marked the passage of the preopercular sensory canal. A supratemporal sensory canal appears to have been present and may have connected with the otic branch of the infraorbital sensory canal within the posterior region of the pterotic. The sensory canal passed medially into the parietal where it opened into a groove on the surface. This groove is continuous across the supraoccipital, and it is assumed that the supratemporal sensory canal was continued within this groove.

The mesethmoid is a short broad bone produced laterally into wings which are attached to the dorsal surface of the vomer. The lateral edges of these wings serve as the articulatory points for the anterior regions of the palatine bones. The anterior edge of the mesethmoid is transversely arranged and the premaxillary pedicels articulated with it.

The lateral ethmoids are small but stout bones, especially ventrally where they provide the posterior articulatory point for the palatine. Laterally the lateral ethmoid provides a further articulatory point for the lachrymal, and dorsally it is attached to the underside of the frontal.

The vomer is separated from the mesethmoid postero-medially but attached to it anteriorly and laterally. The vomer has corresponding lateral wings to those seen on the mesethmoid. A short vomerine process extends back along the ventral surface of the parasphenoid.

The parasphenoid is curved below the orbit and is little expanded ; the lateral regions being simply flattened and inclined ventrally producing a median, ventral longitudinal groove. The ascending process of the parasphenoid curves dorsally to meet the prootic, and has a thickened anterior edge. The foramen which transmitted the internal carotid artery into the base of the orbit lies near to the antero-ventral edge of the ascending process. The posterior part of the parasphenoid, below the myodome, bears a large mid-ventral, curved keel. The parasphenoid joins the ventro-lateral regions of the basioccipital and forms the floor and walls of the myodome. The myodome has a tiny posterior opening between two lateral sheets of parasphenoid below the occipital condyle and above the ventral parasphenoid keel.

The occipital condyle is circular and concave and composed of basioccipital ventrally and of the exoccipitals dorsally. The basioccipital contacts the exoccipitals dorsally, the parasphenoid ventrally and the prootics anteriorly. On the postero-lateral region of the bone near to the condyle is a group of pits and ridges. Internally the basioccipital forms the walls of the posterior part of the otolith chamber, and its ventral surface provides part of the roof of the myodome. Antero-dorsally the

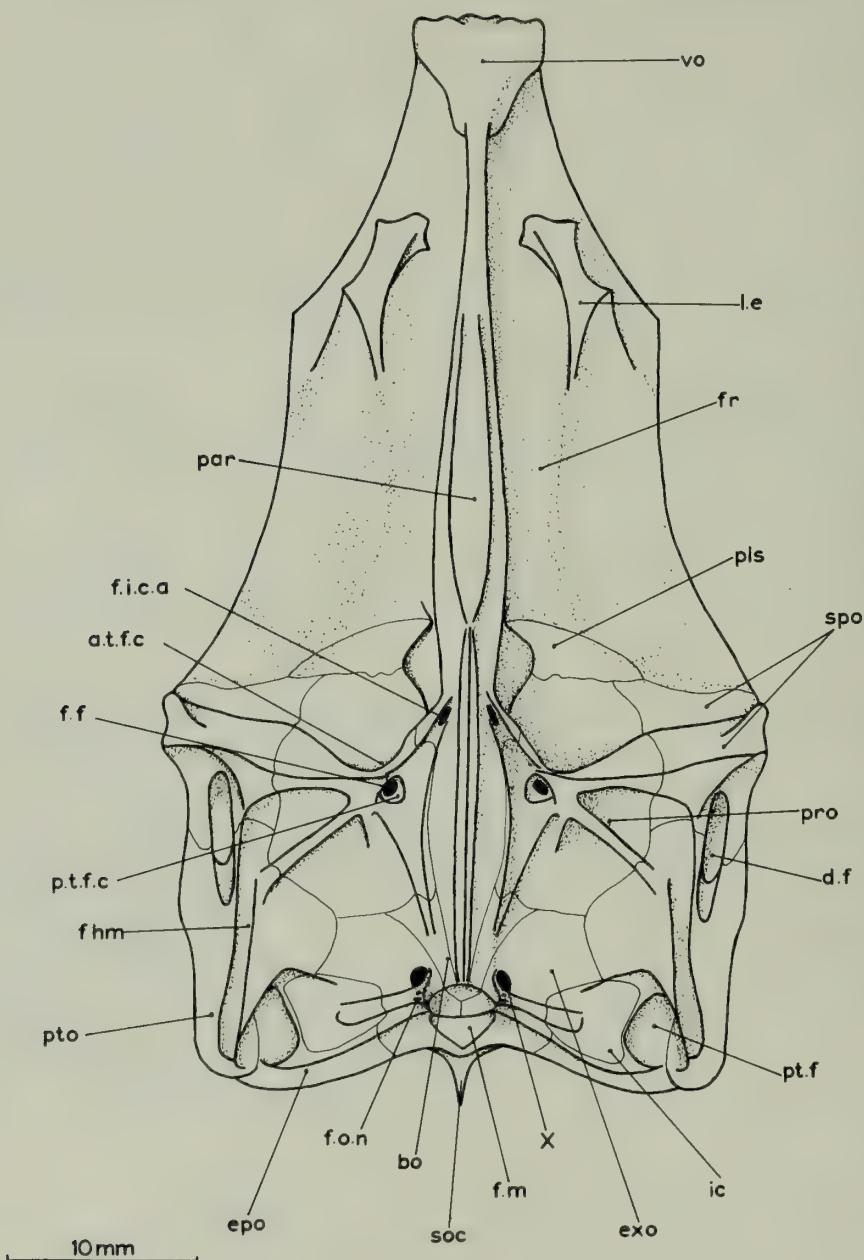


FIG. 50. *Eurypholis pulchellus* (Woodward). Neurocranium in ventral view.

basioccipital contacts the prootic bridge above the myodome. The antero-dorsal extent of the bone provides a partial separation of the two otolith chambers. The otolith chambers themselves extend anteriorly to end in a recess in the prootic just posterior to the internal opening of the facial foramen.

The prootics divide to produce an internal lamina which meets its partner in the mid-line forming the prootic bridge, and an outer lamina which curves laterally in the dorsal region and provides part of the wall of the cranial cavity. Posterior to the prootic bridge the otolith chambers communicate with the cranial cavity through a large oval fenestra. On the orbital face, the prootic meets the sphenotic and pleurosphenoid dorsally. The prootic contains the trigemino-facialis chamber which is divided by bone into a medial pars ganglionaris and a lateral pars jugularis. The pars jugularis is a very short horizontal canal on the lateral face of the prootic which opens anteriorly in the hind wall of the orbit. There is a single foramen leading from the pars ganglionaris into the pars jugularis, the facial foramen, which transmitted the hyomandibular trunk of the facial nerve. The palatine branch of the facial nerve passed through a foramen medial to the facial foramen down into the myodome. The hyomandibular nerve passed out through the posterior opening of the pars jugularis, which also transmitted the jugular vein and the orbital artery. The artery and vein were the only structures which passed through the anterior opening of the pars jugularis. The trigeminal and remaining components of the facial nerve passed through two foramina in the orbital face of the prootic, dorso-medial to the anterior opening of the pars jugularis. The larger of the two foramina is the trigeminal foramen and presumably transmitted all of the remaining branches except the superficial ophthalmics. These latter components passed out through a small foramen dorso-medial to the trigeminal foramen.

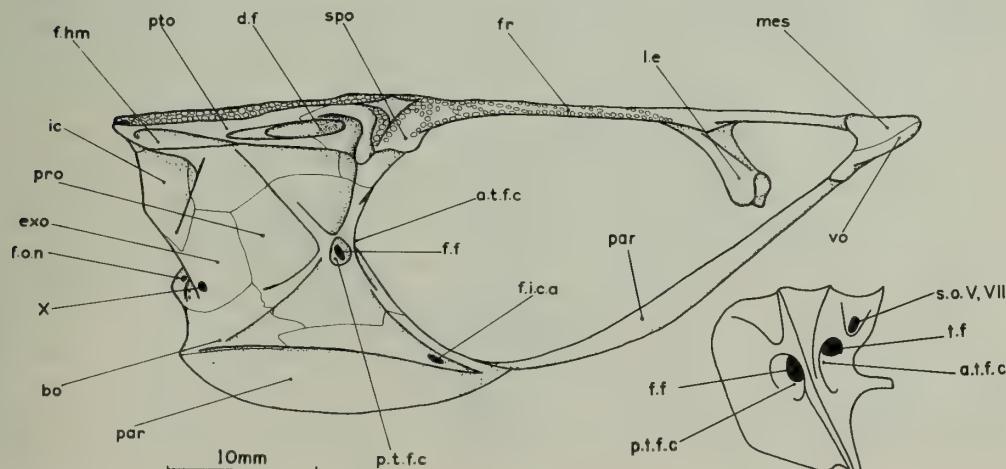


FIG. 51. *Eurypholis pulchellus* (Woodward). Neurocranium in lateral view. The inset shows the prootic in antero-lateral view. From B.M.N.H. number P.10984.

The exoccipital bones meet in the mid-line of the posterior face of the neurocranium below the foramen magnum and just contact each other above it, completely enclosing the foramen magnum. Ventrally each exoccipital contributes towards the composition of the occipital condyle, and laterally forms part of the cranial wall, contacting the intercalar, the pterotic and the prootic. The foramen through which the vagus nerve passed is a prominent hole on the lateral face of the neurocranium in front of the condyle. Between the vagus foramen and the occipital condyle two or three small foramina transmitted the occipital nerves to the anterior region of the vertebral column. Anterior to the vagus foramen on the lateral wall of the cranial cavity a further small foramen is present, which transmitted the glossopharyngeal nerve. Dorsally the exoccipital takes part in the formation of a large concave depression together with the prootic and the pterotic; this depression housed musculature associated with the branchial apparatus. On the posterior face of the neurocranium thickenings of the exoccipital pass laterally to the intercalar and dorso-laterally towards the epiotic.

The pterotic forms almost the entire hyomandibular facet which is an elongate groove on the ventro-lateral surface of the bone. The facet itself is horizontal with the posterior region rising very slightly. Above the hyomandibular facet the dilatator fossa is visible in lateral aspect, its posterior border formed by the pterotic. On the posterior face of the neurocranium a post-temporal fossa is also present and the pterotic forms the lateral parts of the roof, wall and floor of this fossa. The remainder of the roof is composed medially of frontal and parietal with a minute portion of epiotic at the extreme posterior end. The post-temporal fossa is not particularly prominent and is only visible in posterior view.

The sphenotic forms the postero-dorsal orbital region, the most anterior region of the elongated hyomandibular facet and the anterior border of the dilatator fossa. The dorsal part of the sphenotic projects laterally and from the underside of this projection a strut extends ventro-medially to contact a corresponding strut passing dorso-laterally from the prootic, the dorso-lateral strut of the prootic being a direct

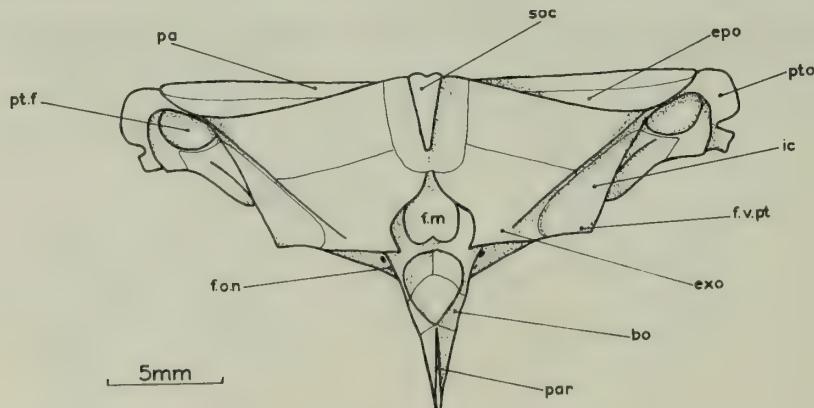


FIG. 52. *Eurypholis pulchellus* (Woodward). Neurocranium in posterior view.
From B.M.N.H. number P.10984.

continuation of the slip of bone forming the lateral wall of the pars jugularis. The anterior region of the hyomandibular facet is immediately behind the strut on the sphenotic.

The epiotic forms much of the posterior face of the neurocranium, and extends on to the extreme posterior end of the skull-roof. Laterally the epiotic enters into the composition of the post-temporal fossa forming the medial parts of the posterior end, i.e. floor, wall and roof. In the floor of the post-temporal fossa it contacts the pterotic and on the posterior face of the skull, below the opening of the fossa, it meets the intercalar.

The intercalar is a moderately large bone forming part of the cranial wall itself. It is bent mesially into a right angle and forms the dorso-lateral continuation of the strut produced on the exoccipital laterally. On the posterior face of the skull it contacts the exoccipital, the epiotic, and dorso-laterally, below the post-temporal fossa, it joins the pterotic. On the lateral face of the neurocranium it contacts the exoccipital and the pterotic below the hind end of the hyomandibular facet. A posterior projecting knob of bone is present on the intercalar representing the point at which the ventral limb of the post-temporal bone attached to the skull.

The pleurosphenoids lie in the dorsal region of the posterior face of the orbit, and contact the frontals above, the sphenotics laterally and the prootics ventrally. The superficial ophthalmic nerves crossed the face of the pleurosphenoid in a slight groove near the medial edge of the bone.

Infraorbital bones. The infraorbital bones are shown in lateral view in Text-figure 54 and differ in no way from those of the type species, *Eurypholis boissieri* (p. 102).

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 53. The hyomandibular is broad, curved and inclined forwards ventrally. The head is elongated antero-posteriorly. The opercular process on the hind edge of the bone is prominent and occurs just within the lower half of the bone. A prominent crest on the lateral face arises near the anterior region of the head and curves postero-ventrally towards the posterior edge, terminating near the ventral extremity. The hyomandibular tapers ventrally. Anteriorly the hyomandibular is thin, expanded and overlain laterally by the metapterygoid. The hyomandibular branch of the facial nerve entered through a large antero-dorsal foramen on the medial face of the bone. Within the bone the nerve divided into the opercular branch, which emerged through a foramen immediately above the opercular process, and the mandibular branch which passed through a foramen situated below the opercular process. The mandibular nerve continued ventrally in a shallow groove on the antero-medial edge of the preoperculum on to the mandible ventrally, below the articular facet.

The symplectic is short, stout and inclined forwards ventrally. Its ventral region lies in a wide groove on the postero-medial part of the quadrate and dorsally it ends close to the ventral extremity of the hyomandibular, to which, in life, it was connected by cartilage.

The quadrate is large and triangular, with a prominent transversely arranged condyle. The bone thins dorsally, but its anterior and posterior regions are thick

and well ossified. The medial groove containing the symplectic is broad and deep and ends just postero-dorsal to the condylar region. The posterior edge of the quadrate lies in a groove on the antero-ventral edge of the preoperculum and is overlapped laterally and medially by the preoperculum. Anteriorly the quadrate is rigidly attached to the postero-medial face of the ectopterygoid.

The ectopterygoid is in two portions joined ventrally, giving a V-shaped dorsal trough between the two components. The ventral edge of the bone is curved and bears teeth. The more posterior teeth are not strictly on the ventral edge of the bone but their bases have moved upwards on to the lateral face of the ectopterygoid. The teeth, however, form a continuous series and are acute, laterally compressed, and hollow. The tooth size decreases towards the posterior end of the bone. All of the teeth have the same angular relation to the supporting bone, i.e. at 90° to it. Therefore the more posterior teeth are directed forwards due to the postero-ventral curvature of the ectopterygoid. All of the teeth are marked by fine longitudinal striations and the bases are expanded and ornamented with small pits and fine striae. The ectopterygoid contacts the postero-ventral surface of the palatine and extends along the medial surface of the latter bone. The palatine thus sits in the groove on the dorsal surface of the ectopterygoid. The medial flange of the ectopterygoid is

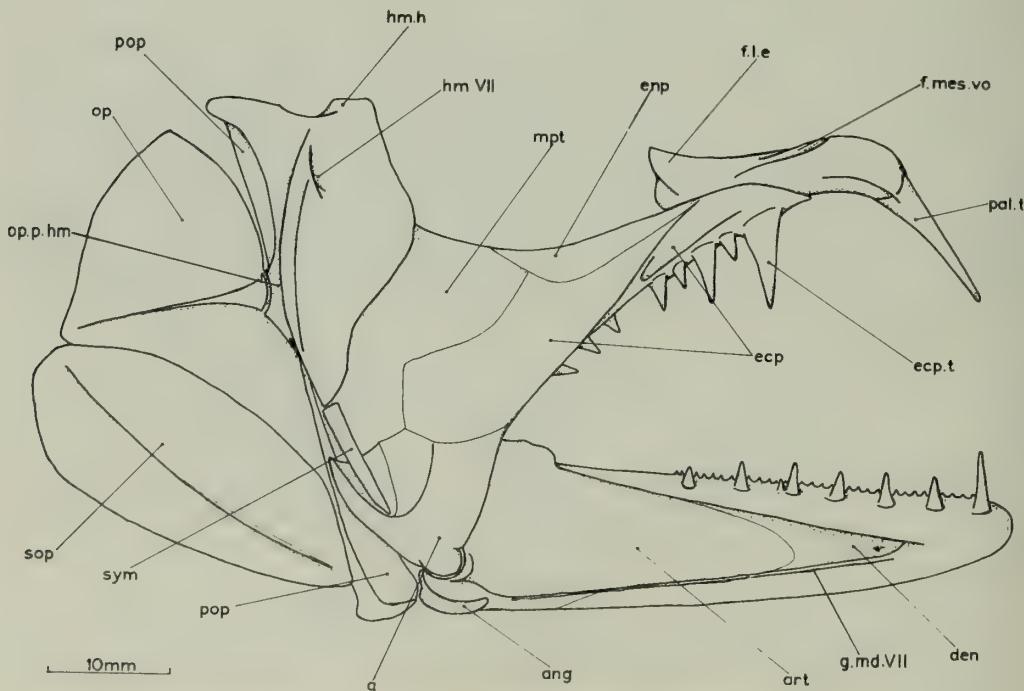


FIG. 53. *Eurypholis pulchellus* (Woodward). Hyopalatine and opercular bones and mandible of the left side in medial view. From B.M.N.H. number P.10984.

larger than the lateral flange and unites dorsally with the lateral edge of the endopterygoid. Posteriorly it is the medial flange which articulates with the quadrate, the lateral flange decreasing in size and merging with the medial one posterior to the last tooth.

The metapterygoid is thin and membranous and missing in parts. Dorsally it lies against the lateral face of the hyomandibular and its outer face bears a shallow obliquely inclined crest which forms the anterior edge of the bone near the ventral limit of the metapterygoid. Antero-ventrally the metapterygoid is attached to the ectopterygoid and the endopterygoid, and ventrally to the dorsal edge of the quadrate.

The endopterygoid is a narrow sheet of bone attached to the innermost edge of the ectopterygoid and lying in the roof of the mouth. The dorsal surface is concave below the orbit, but its convex ventral surface is smooth and untoothed.

The palatine is a prominent, bulbous structure with its posterior end resting in the trough on the dorsal ectopterygoid surface. The palatine bears one enlarged anterior tooth set at 90° to the axis of the bone. The tooth base merges imperceptibly with the palatine bone and the tooth is identical in form to those on the ectopterygoid. Posteriorly the palatine is extended dorsally forming a facet for the reception of the ventral region of the lateral ethmoid. Dorso-medially the palatine has an elongated oval facet which houses the lateral wing formed from the fused lateral extensions of the mesethmoid and vomer.

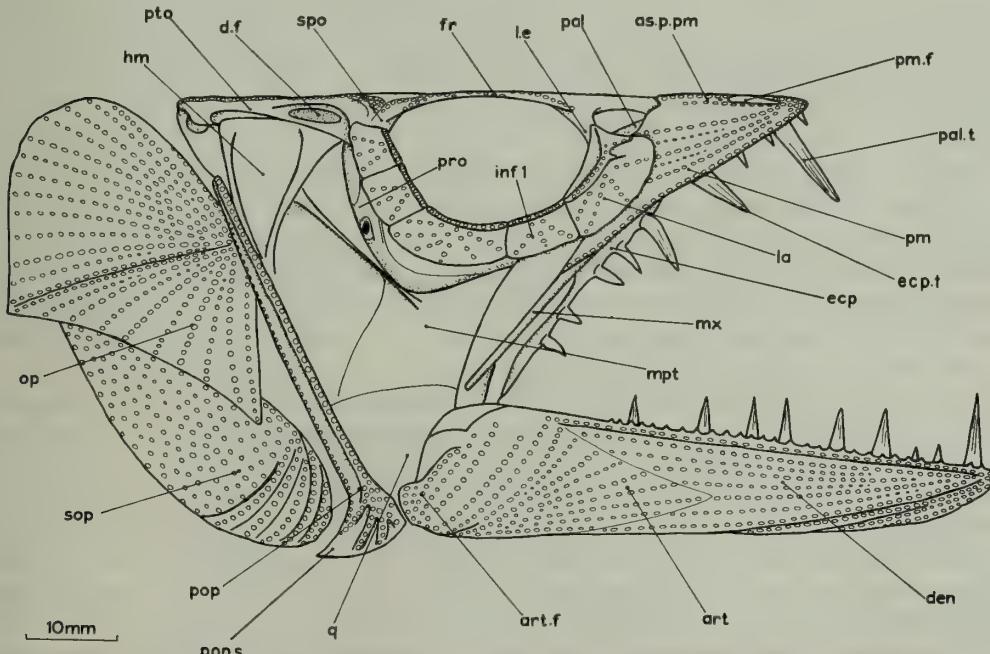


FIG. 54. *Eurypholis pulchellus* (Woodward). Skull of the holotype (B.M.N.H. number P.1703) in lateral view.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 54. The premaxilla is large and has a prominent pedicel anteriorly, lying at 90° to the lateral region of the bone. The premaxillary pedicels meet in the mid-line and lie in the same plane as the anterior part of the skull-roof and form a direct continuation of it, the pedicels articulating with the anterior edge of the mesethmoid. Each pedicel contains an oval fenestra through which the enlarged anteriormost tooth of the dentary projects when the jaws are closed. Between the premaxillary pedicel and the lateral face of the bone there is a groove running to the anterior edge of the snout, this groove is continuous with the anterior opening of the supraorbital sensory canal on the lateral edge of the frontal. The premaxilla is closely associated with the lateral face of the palatine and extends back to a point below the centre of the orbit. The lateral face of the premaxilla is triangular and ornamented with four or five rows of bony tubercles which radiate backwards and outwards from the anterior snout region. Postero-dorsally the lateral face is overlapped by the ventral expansion of the lachrymal bone, and a lateral groove devoid of ornamentation extends anteriorly. This groove may have contained an anterior prolongation of the infraorbital sensory canal. The premaxilla decreases in depth below the lachrymal and tapers posteriorly.

The maxilla enters the gape behind the premaxilla and along its whole length is closely attached to the premaxilla making the demarcation line between the two bones difficult to define. The maxilla is continued on the internal face of the premaxilla and is firmly fused to it. The maxilla is smooth and rod-like with no ornamentation. There is a single marginal row of teeth on the premaxilla which does not extend on to the maxilla. The teeth are small, evenly spaced, acutely pointed and merely seem to be a slightly enlarged marginal row of bony tubercles similar to the tubercular ornamentation on the other dermal bones of the skull.

Mandible. The mandible is shown in medial and lateral views in Text-figures 53, 54. The dentary forms almost the whole of both dorsal and ventral margins of the mandible and over half of the lateral face. The posterior edge of the dentary is deeply indented into a V-shape. The mandible is elongate and relatively shallow with the ventral region strongly inflected towards the mid-line. Dorsally the dentary bears a medial flange on which the teeth are borne in a single row. The teeth are like those found on the palato-pterygoid arcade, i.e., conical, acutely pointed, hollow, slightly recurved, laterally compressed, and with expanded bases. The dentary also bears a ventro-medial flange which diverges from the dorsal flange in the anterior mandibular region. The deep V-shaped groove left between the dorsal and ventral flanges on the internal face of the mandible served to house the remains of Meckel's cartilage.

The articular facet is concave and transverse, limited medially by a small vertical flange, and laterally by a large vertical upgrowth of the articular. This lateral flange completely covers the articular facet so that it is not visible in lateral view. The articular extends anteriorly to occlude the posterior indentation of the dentary, and is inserted on to the medial face of the dentary. The mandibular sensory canal entered the articular region of the mandible behind the articular facet and passed

within the bone ventral to the facet. The tube which contained the sensory canal passes forwards on the ventro-lateral region of the articular and opens into a shallow groove on the posterior region of the dentary. The lateral face of the mandible is ornamented with bony tubercles which run in regular lines radiating backwards from the symphysial region on the dentary, and forwards from the facet region on the articular. The ornamentation is more pronounced antero-ventrally where the tubercles are raised on bony ridges.

The angular is a small knob of bone forming the postero-ventral angle of the mandible.

Opercular bones. The opercular bones are shown in medial and lateral views in Text-figures 53, 54. The preoperculum is deep, narrow and forwardly inclined ventrally. Dorsally it ends behind the head of the hyomandibular where it rests against the posterior face of the crest on the hind edge of the hyomandibular. More ventrally the anterior edge of the preoperculum is excavated vertically, so that a slight concavity is produced into which the posterior edge of the quadrate fitted. Ventrally again the preoperculum is produced into a small backwardly projecting spine. The preopercular sensory canal ran within a tube in the bone opening dorsally by a single pore, and ventrally by two or three pores. Two of the ventral pores open posteriorly on the region of the spine, whilst the most anterior pore opens anteriorly on to the articular. The lateral face of the preoperculum is ornamented with characteristic bony tubercles which are more prominent in the region above the sensory canal and along the posterior margin of the bone. Ventrally on the preopercular spine the tubercles are raised on ridges of bone.

The operculum has a straight anterior edge covered by the preoperculum laterally. The dorsal border of the operculum is rounded but ventrally the edge is concave. From the articulatory facet midway along its anterior edge an internal horizontal strengthening ridge crosses the bone and terminates on the posterior angle where it is produced into a short spine. Laterally the operculum is ornamented with radiating rows of bony tubercles arising from the point of articulation with the hyomandibular.

The suboperculum is large with its dorsal part lying medial to the ventral region of the operculum. The lateral face of the bone is ornamented with a regular arrangement of bony tubercles.

Genus *SAURORHAMPHUS* Heckel, 1850

DIAGNOSIS (emended). Eurypholidae in which the head is elongated, especially in the preorbital region where it is extended into a prominent rostrum. Vertebral number 42 of which 22 are caudal. Body very shallow, never exceeding the depth of the head, and extended by an increase in the length of the individual centra especially precaudally. Pelvic fins and pectoral fins of equal size; pelvic fin almost subthoracic in position. Mid-dorsal scutes 6 or 7 in number, overlapping each other in advance of the dorsal fin.

TYPE SPECIES. *Saurorhamphus freyeri* Heckel.

REMARKS. The genus *Saurorhamphus* is known by this single species originally described by Heckel (1850). Woodward (1901 : 210) transferred it to the genus *Eurypholis* but this was later shown by d'Erasmo (1912 : 87) to be incorrect, *Saurorhamphus* representing a distinct genus closely associated with *Eurypholis*. This latter conclusion is substantiated in the following description.

***Saurorhamphus freyeri* Heckel**

(Text-fig. 55)

1850 *Saurorhamphus freyeri* Heckel : 217, pls. 18, 19.

1946 *Saurorhamphus freyeri* Heckel ; d'Erasmo : 92, text-fig. 24.
d'Erasmo lists the earlier references.

DIAGNOSIS (emended). *Saurorhamphus* of standard length up to 18 cm. Length of head with opercular apparatus just over three times the depth of the head, equal to one-third of the standard length. Maximum depth of the mandible equal to one-seventh of the total length. Maxilla forms one-third of the oral border of the mouth and is untoothed. Operculum broader than deep. Dorsal fin in the mid-trunk region with 14 rays. Anal fin remote, with 15–16 rays arising well behind the dorsal fin, close to the caudal fin.

HOLOTYPE. Complete flattened fish wanting snout, in the Natural History section, Prirodoslovni Muzej Slovenije, Ljubljana, Jugoslavia, from the Lower Cenomanian of Comen, near Trieste.

MATERIAL. Only the holotype in Ljubljana was examined since none of the specimens used by d'Erasmo (1912, 1946) could be traced.

DESCRIPTION. *Neurocranium*. The posterior region of the skull-roof is the only part of the neurocranium which is at all well shown. The frontals occupy practically the entire roof, reaching back almost to the occiput. They are long and narrow and attain their greatest width at the rear end of the orbit above the sphenotic. The skull-roof is flat and ornamented with a regular arrangement of bony tubercles which radiate in all directions from the centre of ossification on the frontal. Anteriorly the frontal tapers gradually from the front end of the orbit and is inserted into the hind end of the mesethmoid.

The supraoccipital is small and separates the transversely arranged parietals. It bears no indication of having had a supraoccipital crest, but each parietal bears a shallow, transverse, ornamented crest. The tubercular ornamentation seen on the frontals is continued on to the parietals and the supraoccipital.

The pterotic forms the postero-lateral border of the skull-roof and dorsally appears as a narrow elongated strip of bone extending anteriorly on to the dorsal surface of the sphenotic. Posteriorly it projects slightly behind the level of the occiput and its dorsal surface is ornamented with bony tubercles.

The sphenotic forms the postero-dorsal region of the orbit and projects laterally from beneath the frontal. Unlike the other roofing bones the sphenotic is unornamented.

The epiotics are present on the occipital border of the skull-roof as smooth hemispherical protuberances providing an articulatory surface for the dorsal limb of the post-temporal.

Infraorbital bones. Traces of a circumorbital series of bones can be seen. The bones which are visible bear an external ornamentation of bony tubercles. Beneath the orbit there is a long shallow bone probably representing the first infraorbital, and behind this there is a larger bone (2nd infraorbital) which is angled and slightly more expanded and which shows the tube which housed the sensory canal.

Jaws and suspensorium. The hyomandibular is large with a greatly elongated head. Ventrally the hyomandibular curves forwards so that the mandibular articulation lies below the centre of the bone. The lateral face of the hyomandibular is covered to a large extent by the postero-dorsal region of the metapterygoid.

The anterior region of the head is only present as an impression in the matrix so that description is rendered difficult. The ectopterygoid would seem to be greatly extended as is also the palatine. The ectopterygoid bears a longitudinal series of evenly spaced teeth, but the dentition of the palatine is difficult to determine. At the anterior end of the rostrum an impression of a palatine tooth is visible. It is large and extends downwards over the impression of the lower jaw. Whether further palatine teeth were present cannot be observed on the specimen. No corresponding enlarged tooth of the dentary at the symphysis is present. Within the orbit, below what appears to be parasphenoid, the endopterygoid forms a flattened lamina of bone. The parasphenoid in the orbital region is slightly expanded ventro-laterally.

The dermal upper jaw is only present as an impression in the rock. The premaxilla appears to be elongated and large, extending posteriorly to the orbit and bearing a lateral ornamentation of bony tubercles. The maxilla enters the oral edge of the upper jaw below the orbit. The premaxilla is toothed marginally but the maxilla appears to be untoothed.

The mandible is prominent, elongate, relatively shallow and with a constricted symphysis. The lateral face is covered with a dense ornamentation of raised bony tubercles. The suture between the dentary and the articular could not be observed in the specimen. A dorsal extension of the articular lateral to the articular facet extends upwards and hides the facet and the quadrate condyle in lateral view. The retroarticular process is insignificant, and the coronoid process is low. The mandibular dentiton was not observed in the specimen.

The preoperculum is deep and narrow although there are anterior and posterior expansions ventrally. The anterior edge of the bone follows the anterior curvature of the hyomandibular and the quadrate, and abuts against the posterior edges of both of these bones. Postero-ventrally there is a slight backwardly projecting spine. The lateral face of the preoperculum is ornamented with a uniform covering of bony tubercles. The operculum is large and about as deep as long with a straight anterior edge. The facet for the articulation with the hyomandibular is midway down the anterior edge of the bone. The dorsal edge of the operculum is rounded and the margin is produced posteriorly into a short spine. Ventrally the

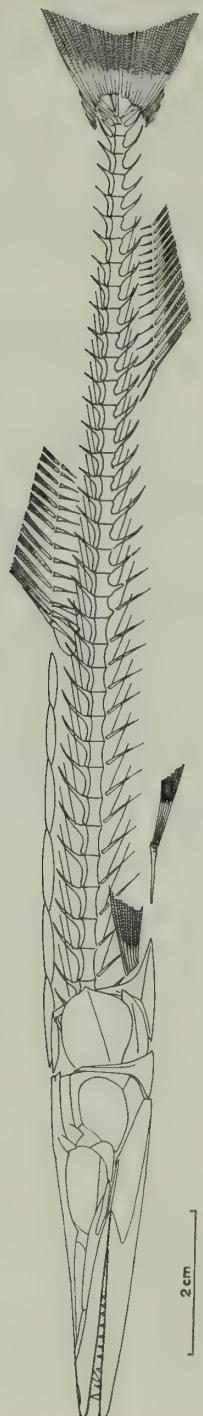


FIG. 55. *Saurorhamphus freyeri* Heckel. Restoration of the skeleton, lateral line scales omitted but dorsal scutes in position.

margin of the operculum is straight and slightly oblique. An inner strengthening ridge runs from the region of the facet anteriorly and traverses the medial face of the bone to terminate on the small posterior spine. The suboperculum is prominent and like the operculum bears an inner strengthening ridge. Both bones are ornamented with tubercles, those on the operculum radiating outwards from the anterior edge of the bone in the region of the opercular facet.

Pectoral and pelvic girdles and fins. The post-temporal has an oval upper limb whose dorsal surface is ornamented with tubercles. The supracleithrum could not be seen since it lies medial to the upper opercular region. The cleithrum is large and ventrally it is expanded both anteriorly and posteriorly. The anterior end of the cleithrum almost reaches the preoperculum, while the posterior end projects backwards beyond the insertion of the pectoral fin. Ventrally the lower margin of the cleithrum is inflected towards the mid-line. The lateral face of the cleithrum bears the same tubercular ornamentation as the opercular bones and the tubercles are more pronounced ventrally. The pectoral fin arises just below the middle of the flank and appears to consist of approximately 12 rays forming a moderately large fin.

The pelvic bones are prominent and each consists of a thin sheet of bone roughly triangular in shape. The pelvic bones lie immediately posterior to the cleithrum and thus can be said to be sub-thoracic in position. The pelvic fins are as large as the pectoral fins and are composed of 7 or 8 stout rays.

Median fins and tail. The dorsal fin is situated behind the mid-point of the body and is composed of 14 rays. The first ray is small and unbranched, the second ray is the longest and the remaining rays decrease in length. All the rays are segmented, and except for the first are branched. The pterygiophore number parallels the number of fin rays, and the first 3 proximal radials are expanded, especially the first which bears an expanded anterior median keel. The anal fin is remote and consists of 15 or 16 rays; unlike the dorsal fin, none of the proximal radials is expanded.

The caudal fin consists of 19 principal rays. Accessory caudal rays are present in front of the principal rays both above and below the fin, there being between 18–20 in all.

Vertebral column. The vertebral column has some 41 or 42 vertebrae of which approximately 22 are caudal. In the anterior precaudal region the first few centra are long and narrow and mesially constricted. The centra begin to shorten in length at about the 10th precaudal vertebra and by the 14th precaudal vertebra they have become reduced to a length which remains constant to about the 13th caudal (the 34th vertebra). From this vertebra to the end of the column the centra become further reduced in length and depth so that at the caudal peduncle the centra are very small and practically square. The neural arches are prominent and the line of articulation between the arch and the corresponding centrum is clearly visible. The neural spines are short and arise from the posterior region of each neural arch. In the precaudal region the neural spines are at their longest and exhibit a slight backward curvature. Below the dorsal fin the spines shorten and straighten, and

along the caudal region become progressively shorter. Small transverse processes are present on the precaudal vertebrae, supporting fine pleural ribs. The haemal spines are short but slightly more curved than the corresponding neural spines of the caudal region.

Intermuscular bones are present along practically the entire length of the body, epineurals dorsally and epipleurals ventrally.

Scales. Scales are only present along the lateral line and in the mid-dorsal line behind the occiput. These latter scutes may be as many as six in number and are large, ovoid, and ornamented with a median longitudinal ridge as well as concentric rings of minute tubercles. These scutes may have contained a branch of the sensory canal system from the head. The third scute in particular shows a postero-dorsal pore in the median ridge. The lateral line scales begin just posterior to the post-temporal bone where they are very large, more posteriorly they decrease in size progressively. The scales overlap and there are approximately 42 scales in the row. Each scale is irregularly triangular with the base of the triangle directed posteriorly. This posterior edge bears a deep, narrow indentation. This indentation occurs where the scale overlaps the anterior region of the succeeding scale. The lateral surface of each of the scales is ornamented with raised tubercles except in the overlapped portion.

Suborder HALECOIDEI

DIAGNOSIS. Head and body shallow to slightly deepened. Parietals separated in the mid-line by the supraoccipital. Post-temporal fossa unroofed. Orbitosphenoid and basisphenoid absent ; supraorbital often present. Premaxilla toothed, with no ascending process, maxilla always with forwardly inclined teeth ; one supramaxilla present. Teeth on palatines, ectopterygoids and endopterygoids but not on vomer. Numerous branchiostegal rays. Mesocoracoid arch present ; pectorals inserted low on body. Pelvics abdominal or sub-thoracic. Vertebral elements incompletely fused ; epineurals numerous. Fins without spines. Caudal with 17 branched rays. Preural vertebra 1 fused with ural vertebra 1 ; ural vertebra 2 present as a terminal half-centrum. Scales present or absent, when present small and closely packed.

Family HALECIDAE Agassiz, 1834

DIAGNOSIS. Head and body tending to become shortened and deepened. Maxilla forms at least half of the gape and bears large, forwardly inclined teeth ; characteristically small supramaxilla always present. Preopercular spine arising from the postero-ventral region of the preoperculum. Dorsal fin confined to the anterior half of the back. Anal fin always remote in position.

Genus HALEC Agassiz, 1834

DIAGNOSIS (emended). Halecidae in which the head is short and undepened and the body is slightly elongated. Supraorbital present. Jaw suspension vertical.

Branchiostegal rays at least 15 in number. Vertebrae between 40 and 46. Pelvic fins abdominal, equal in size to the pectorals. Epineurals on the first 30 vertebrae. Complete covering of minute scales, enlarged along the lateral line.

TYPE SPECIES. *Halec sternbergi* Agassiz.

REMARKS. The family Halecidae was originally erected, as the name implies, to include the 'herring-like' forms, the clupeoids and the salmonoids. The grouping together with the familial name was dropped later on, although used by Pictet (1850) and Davis (1887). The family is re-erected but only to contain three genera. Of the genus *Halec*, two species are considered, *Halec eupterygius*, preserved 'in the round', and *Halec haueri* which is always laterally flattened.

***Halec eupterygius* (Dixon)**

(Text-figs. 56-62)

1837 *Osmeroïdes lewesiensis* Agassiz, 5; 1: pl. 6ob, figs. 3, 4 (*errore*).

1850 *Pomognathus eupterygius* Dixon: 367, pl. 35, figs. 6, 7.

1888a *Pomognathus eupterygius* Dixon; Woodward: 318.

1901 *Halec eupterygius* (Dixon); Woodward: 213.

1902 *Halec eupterygius* (Dixon); Woodward: 50, pl. 13, text-fig. 11.

DIAGNOSIS (emended). *Halec* species reaching approximately 31 cm. in standard length. Length of the head with the opercular apparatus exceeds the depth of the trunk, and is contained four times in the length from the pectoral arch to the base of the caudal fin. Vertebrae 45 in number, at least 20 and possibly 22 being caudal. Dorsal fin triangular, with 12 rays, first rays stout and ornamented; anal fin small and remote.

HOLOTYPE. Imperfect fish in the Brighton Museum from the Turonian of south-east England.

MATERIAL. Specimens in the B.M.N.H., listed by Woodward (1901: 213-218), totalling some 30 specimens. Neurocranial description obtained from specimen numbers P.36237, P.4289, P.10920, and 43392 all of which were prepared in acetic acid. The specimens are from the Turonian and Senonian stages of south-east England.

DESCRIPTION. *Neurocranium*. The neurocranium is shown in dorsal, ventral, lateral and posterior views in Text-figures 56-59. The cranial roof is flattened and widest at the hind border of the orbit between the sphenotics. The orbital region is large and the parasphenoid is slightly curved below it. The major portion of the roof is formed from the frontals which extend back almost to the occipital border, and meet in the mid-line in a practically straight suture. Postero-laterally a small V-shaped indentation of the frontal marks the anterior limit of the post-temporal fossa. The frontal does not extend into the floor of the post-temporal fossa. Laterally the frontal overlaps the dorso-medial surface of the sphenotic, but the major part of the sphenotic still projects laterally from beneath it. The dorsal surface of the frontal is ornamented with finely tuberculated ridges radiating from the centre of ossification. This ornamentation is absent from the anterior and medial regions of the

frontals. Anteriorly the frontal tapers very slightly to end at the rear of the short, broad, smooth mesethmoid.

The supraorbital sensory canal ran within the frontal above the orbit, and gave off a branch which opened through a medial pore at the level of the centre of the orbit. The main supraorbital canal opened anteriorly on the edge of the frontal.

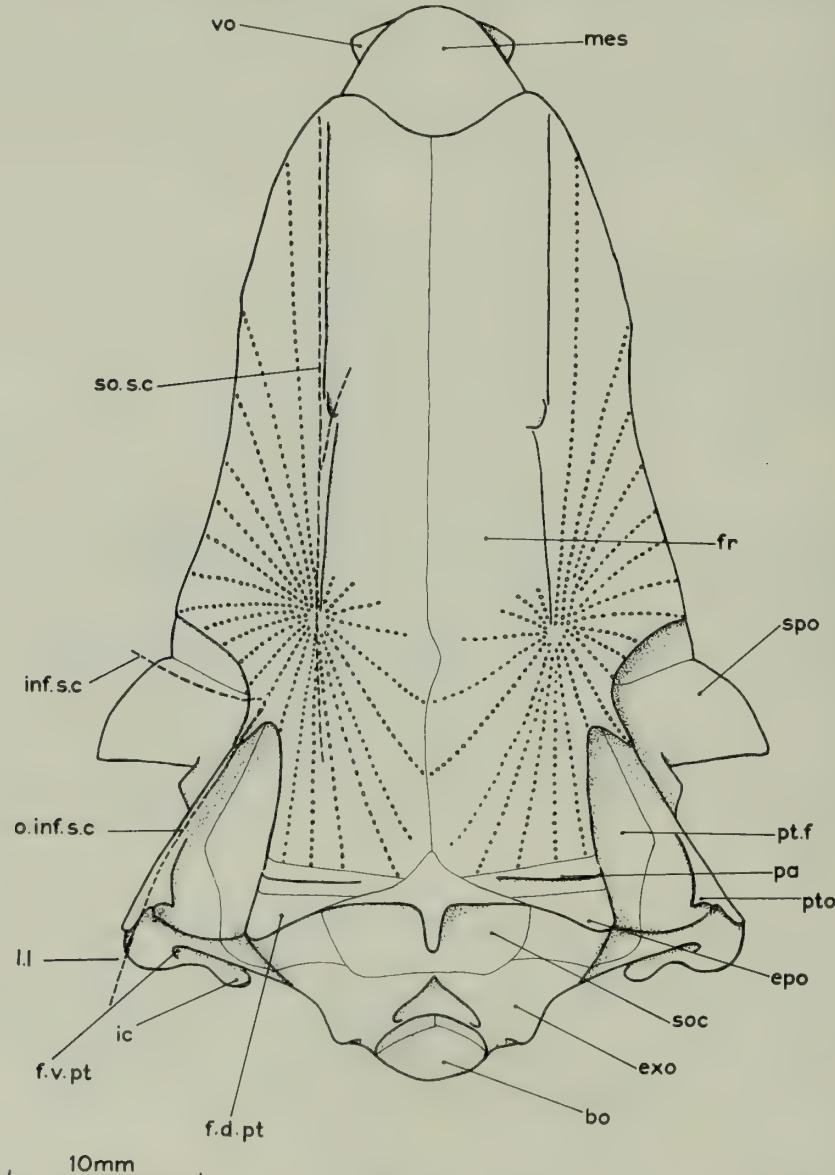


FIG. 56. *Halec eupterygius* (Dixon). Neurocranium in dorsal view. The broken line on the left side of the figure indicates the course of the sensory canals.

The supraoccipital is a small bone just appearing on the dorsal surface of the neurocranium. It is overlapped anteriorly by the frontals, and separates both the parietals and the epiotics. A small backwardly directed crest is produced which does not extend above the plane of the skull-roof.

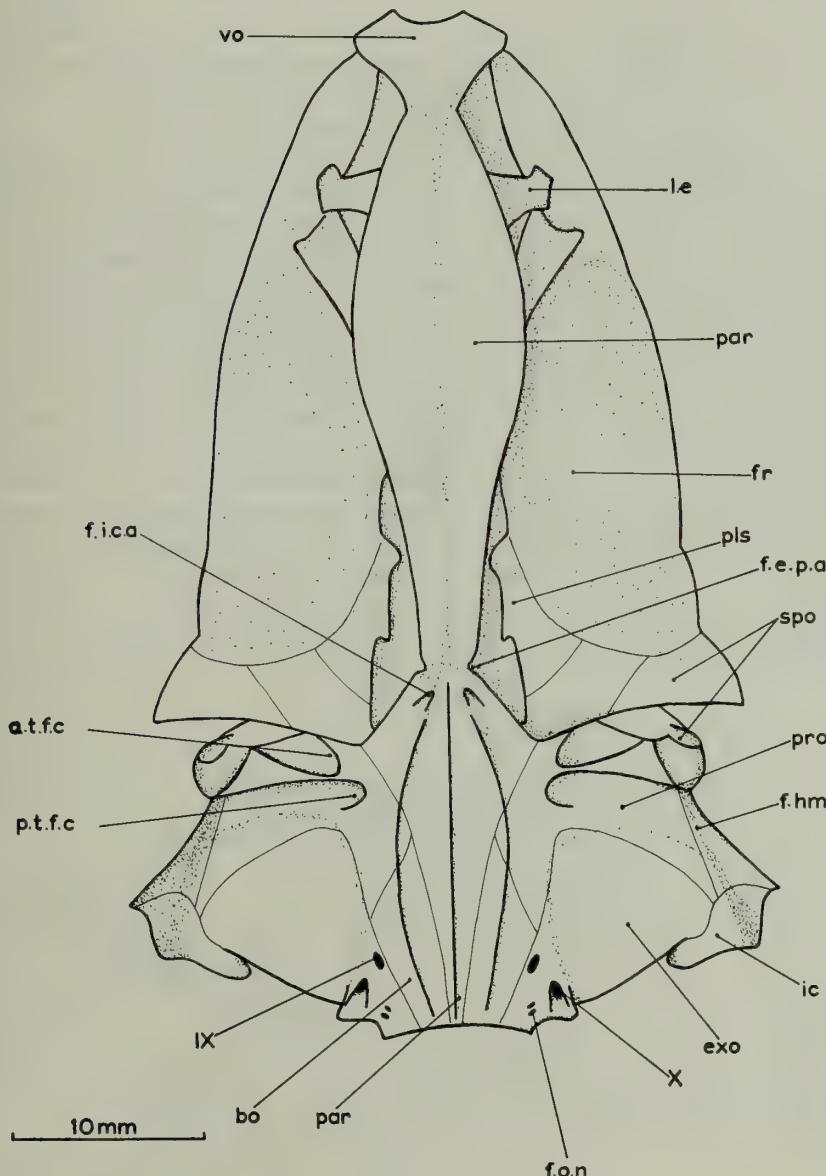


FIG. 57. *Halec eupterygius* (Dixon). Neurocranium in ventral view.

The parietals are narrow, transversely orientated strips of bone, at the hind end of the frontals. Each parietal bears a small transversely arranged parietal crest, but the remainder of the surface is smooth.

The mesethmoid is short, broad and poorly ossified, but internally thin membranous sheets of bone extend back to the lateral ethmoids. Laterally the mesethmoid is attached to the vomer.

The lateral ethmoids are flimsy bones representing merely superficial ossifications of cartilaginous components. The lateral and ventral regions of the lateral ethmoid are however more strongly ossified than the remainder. Ventrally the lateral ethmoids are attached to the postero-dorsal region of the palatine.

A small supraorbital bone lies along the lateral edge of the frontal above the lateral ethmoid. The supraorbital is oval and finely ornamented with small tubercles.

The vomer, which attaches to the undersurface of the mesethmoid, is a small shallow bone with a short posterior process. This posterior process extends backwards below the anterior end of the parasphenoid. The vomer is expanded laterally and between the mesethmoid and vomer the head of the maxilla articulates.

The parasphenoid extends for practically the entire length of the neurocranium. Below the orbit it widens considerably and consists of a pair of large ventro-laterally inclined flanges associated with the endopterygoids. The ascending processes of the parasphenoid curve upwards at the posterior end of the orbit to meet the prootics in the walls of the myodome. The anterior edge of each ascending process is thickened. The course of the efferent pseudobranchial artery is represented by a notch in the antero-ventral edge of the ascending process. The foramen for the internal carotid artery lies just behind the efferent pseudobranchial notch. Posteriorly the parasphenoid joins the basioccipital. The parasphenoid terminates just in front of the hind end of the basioccipital and forms the complete floor of the myodome.

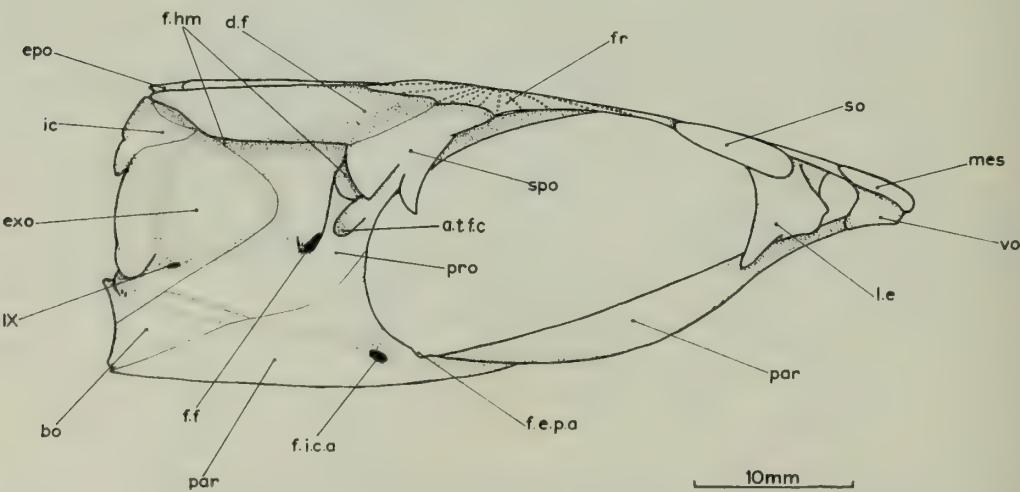


FIG. 58. *Halec eupterygius* (Dixon). Neurocranium in lateral view.

The occipital condyle is circular and concave and formed of both basioccipital and exoccipitals. The basioccipital contacts the exoccipitals dorsally and the prootics antero-dorsally. Internally the basioccipital forms the walls of the posterior parts of the otolith chambers and the roof to the posterior myodome. The otolith chambers extend anteriorly to terminate in a recess within the prootic, lateral to the prootic bridge.

The prootic extends medially to meet its partner forming the prootic bridge above the myodome. Dorso-laterally the prootic contacts the sphenotic within the anterior cup-shaped part of the hyomandibular facet. The orbital face of the prootic, above the prootic bridge, meets the sphenotic dorso-laterally, the frontal dorsally and the pleurosphenoid dorso-medially. The pars ganglionaris is a shallow medial recess in the prootic, lateral to the prootic bridge. The pars jugularis is a short horizontal canal lateral to the pars ganglionaris. Two foramina pass from the pars ganglionaris into the pars jugularis. The anterior foramen is the trigeminal foramen, the more posterior the facial foramen. The hyomandibular nerve passed through the facial foramen into the pars jugularis and out through the posterior opening of the pars jugularis. The anterior opening of the pars jugularis is separated from the posterior opening by a narrow splint of bone. The posterior opening transmitted the hyomandibular nerve, the jugular vein, and the orbital artery. The palatine nerve did not enter the pars jugularis but passed through a small foramen medial to the facial foramen down into the myodome. The anterior opening of the pars jugularis is a vertically elongated slit-like aperture through which passed the jugular vein, the orbital artery, and the remainder of the trigeminal and facial nerves.

The exoccipitals meet above and below the foramen magnum and each contributes to the occipital condyle. Laterally the exoccipital has a prominent foramen which transmitted the vagus nerve, the opening being slightly overhung by a flange of bone. The glossopharyngeal foramen is smaller and just anterior to the vagus foramen. Both of these foramina lie within a groove extending from the posterior part of the exoccipital to the posterior opening of the pars jugularis on the prootic. Lateral to the occipital condyle and immediately below the vagus foramen, two or three very small foramina transmitted the occipital nerves. Laterally the exoccipital is deeply excavated into a membranous concave depression which housed pharyngeal musculature. On the posterior face of the skull the exoccipital meets the supraoccipital dorso-medially and the epiotic dorsally and dorso-laterally.

The pterotic bears a dorsal crest forming the outer wall of the post-temporal fossa. On the lateral face of the neurocranium the pterotic joins the sphenotic and prootic in the hyomandibular facet. The more posterior part of the hyomandibular facet is made up of the pterotic alone. The otic branch of the infraorbital sensory canal passed within the pterotic crest opening anteriorly above the sphenotic. The pterotic crest also delimits the dilatator fossa which is an excavation of the dorso-lateral surfaces of both the sphenotic and pterotic.

The intercalar is a small bone, superficial in position, covering part of the suture between the exoccipital and pterotic. The intercalar is wrapped around the

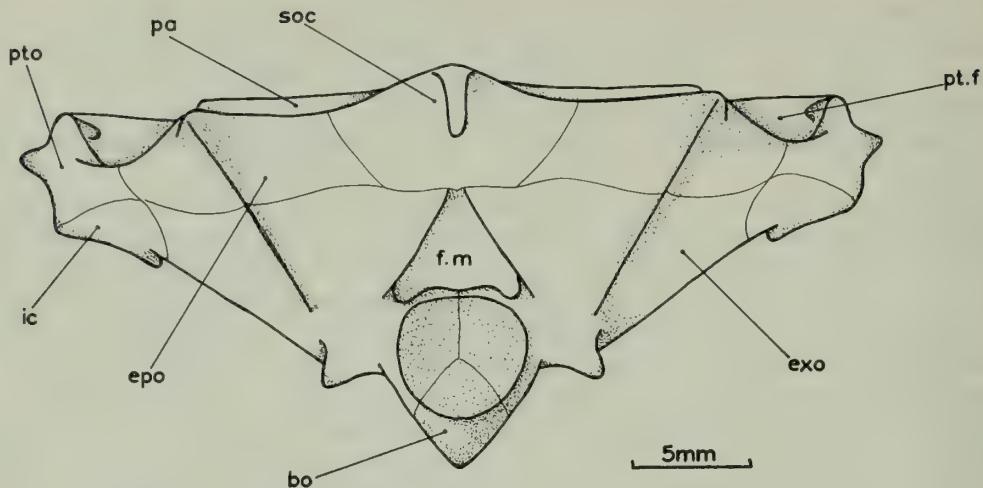


FIG. 59. *Halec eupterygius* (Dixon). Neurocranium in posterior view.

posterior angle of the lateral face of the neurocranium, and is thus visible both in posterior and lateral views. Postero-dorsally the intercalar has a facet for the ventral strut of the post-temporal.

The sphenotic is large and well ossified and forms the postero-dorsal corner of the orbit. The sphenotic projects ventro-laterally from beneath the frontal contacting the pterotic posteriorly and the prootic ventrally. The epiotics appear on both dorsal and posterior surfaces of the neurocranium and are separated medially by the supraoccipital. The epiotic enters into the composition of the post-temporal fossa forming part of the medial wall and floor. The upper limb of the post-temporal articulates with the dorsal surface of the epiotic, medial to the posterior end of the post-temporal fossa.

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 60. The hyomandibular is large with a double head. The opercular process is ill-defined and approximately midway down the rear edge of the bone. The lateral face of the hyomandibular has a prominent lateral crest arising from the anterior head region and passing postero-ventrally to the rear edge of the bone. The preoperculum rests against the posterior face of this crest. The crest gradually shallows and disappears near to the ventral extremity of the bone. The anterior extent of the hyomandibular is thin and membranous and covered laterally by the metapterygoid. The hyomandibular tapers ventrally where it is circular in cross-section. The hyomandibular branch of the facial nerve entered the bone through an antero-dorsally directed foramen just below the head. Within the bone the nerve divided; the opercular nerve came out near to the opercular process on the rear edge of the bone; the hyoidean and mandibular nerves passed through foramina below the opercular process and continued ventrally on the posterior edge of the hyomandibular.

The symplectic is small and inclined forwards ventrally. Dorsally it is separated from the hyomandibular and ventrally lies in a groove on the posterior part of the medial face of the quadrate.

The quadrate is a large triangular bone with a transversely orientated condyle at its ventral angle. The groove which housed the symplectic is long and shallow and ends just behind the condyle. The postero-dorsal corner of the quadrate is emarginated. The posterior edge however is thickened and slightly grooved to house the leading edge of the preoperculum. Dorsally the quadrate meets the metapterygoid and anteriorly the ectopterygoid.

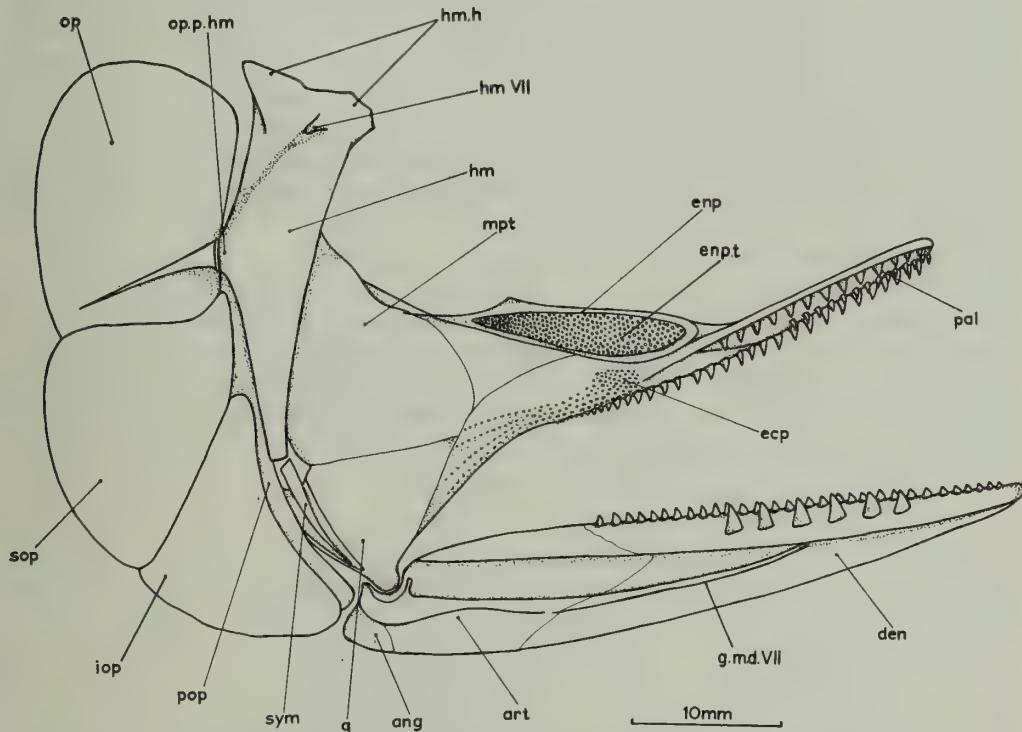


FIG. 60. *Halec eupterygius* (Dixon). Hyopalatine and opercular bones and mandible of the left side, medial view.

The metapterygoid is large, thin and membranous. On its lateral face it has a crest which originates antero-ventrally and passes postero-dorsally. More dorsally this crest marks the anterior edge of the metapterygoid.

The ectopterygoid is bent through a slight angle posteriorly where it extends below the anterior part of the quadrate. The anterior end of the ectopterygoid abuts against the palatine and the dorsal edge contacts the endopterygoid. Teeth are present on the ectopterygoid and are of two types. The first are prominent marginal teeth which decrease in size posteriorly where they also become closely crowded. These teeth are acutely pointed, recurved and with a slight lateral

compression. Fine longitudinal striations are present on the teeth and on the expanded bases. The second type of teeth on the ectopterygoid are minute and collected into a patch posteriorly. The ectopterygoid meets the palatine anteriorly in an elongated suture, extending forwards alongside the palatine.

The endopterygoid is thin and membranous, meeting the metapterygoid posteriorly. The ventral surface of the endopterygoid is convex and supports a large oval tooth-patch.

The palatine is prominent and bears three rows of large teeth, identical in form to those on the ectopterygoid. Posteriorly the palatine tapers to fit between the ectopterygoid and endopterygoid. At the posterior end the teeth on the palatine are reduced to a single row. The tooth row on the ectopterygoid is continuous with the most lateral tooth row on the palatine. In this outer tooth row the teeth decrease in size anteriorly and posteriorly. The central row of teeth are smaller and more irregular both in size and position. The innermost tooth row extends the entire length of the palatine and has the largest teeth in the upper jaw. The dorsal surface of the palatine is longitudinally grooved for the reception of the ventral expansions of the lateral ethmoid. Anteriorly the palatine is associated with the lateral edge of the vomer.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 61. The premaxilla is elongate and forms the majority of the oral border. The anterior region is expanded where it wraps around the front end of the snout to contact its partner of the other side. This expanded region is ornamented with numerous, evenly spaced, minute tubercles. Posteriorly the premaxilla is long and

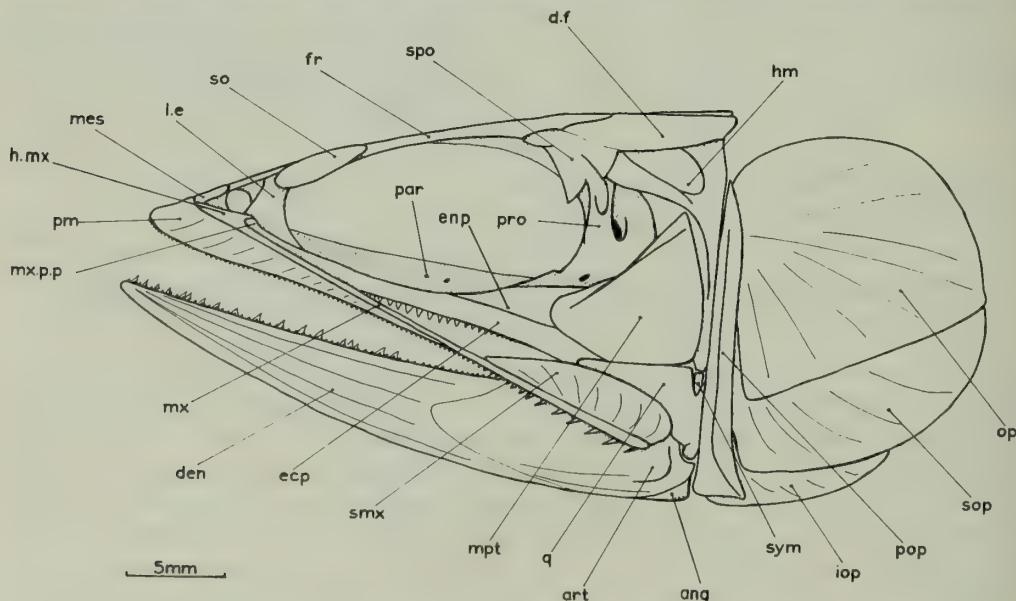


FIG. 61. *Halec eupterygius* (Dixon). Restoration of the skull in lateral view.

slender, lying beneath the maxilla. The complete oral edge of the premaxilla has a fringe of minute conical teeth.

The maxilla is also long and thin and along most of its length is closely associated with the premaxilla. The anterior part of the maxilla curves inwards and this medial region is associated with a very small maxillary process on the dorsal surface of the palatine. Anteriorly the maxilla also articulates with the vomer and the mesethmoid. The maxilla enters the gape posterior to the premaxilla, and supports a row of teeth. These teeth are enlarged, well spaced and inclined forwards.

The maxilla supports a single supramaxilla which is elongate and pointed anteriorly. The lateral face of the supramaxilla is ornamented with radiating tuberculated ridges.

Mandible. The mandible is shown in medial and lateral views in Text-figures 60 and 61. The dentary forms the greater part of both dorsal and ventral edges of the mandible, and is constricted at the symphysis. The oral margin of the dentary is produced into a medial tooth bearing flange. The teeth are arranged in two rows, a marginal row of smaller teeth and an inner row of larger ones. These teeth are identical in form to those on the palato-pterygoid.

The articular forms the posterior part of the dorsal border of the mandible as well as part of the ventral border and lateral face. The articular facet is concave and transversely orientated. The articular extends anteriorly on to the medial face of the dentary. The mandibular sensory canal ran within a tube in the ventro-lateral region of both the articular and dentary. The lateral face of the mandible is smooth dorsally, but ventrally is ornamented with small tubercles. The angular is a small knob of bone attached to the postero-ventral region of the articular.

Opercular bones. The opercular bones are shown in medial and lateral views in Text-figures 60 and 61. The preoperculum is long and narrow with a slight forward curvature ventrally. The upper limit of the bone lies behind the hyomandibular head whilst the anterior edge rests against the rear edges of both the hyomandibular and the quadrate. The preopercular sensory canal ran in a groove on the lateral face of the bone. The flange overhanging the groove is ornamented with ridges and tubercles. This ornamentation continues on the lower end of the bone.

The operculum has an irregularly concave ventral edge. From the articular facet an internal horizontal strengthening ridge crosses the operculum to terminate on the posterior edge. The lateral face of the operculum is ornamented with minute tubercles radiating outwards from the region of the opercular facet. The suboperculum is large and deep with its dorsal edge covered by the ventral part of the operculum. Ventrally the suboperculum is thin and membranous and has an ornamentation of bony tubercles. The interoperculum lies medial to the ventral part of the preoperculum, and has a similar ornamentation to the other opercular bones.

Pectoral girdle and fin. The pectoral girdle is shown in medial view in Text-figure 62. The post-temporal has a large, plate-like upper limb articulating with the epiotic, and a shorter strut-like ventral limb articulating with the intercalar. The supracleithrum articulated with the posterior region of the post-temporal, and the

lateral line sensory canal passed through the head of the supracleithrum and the post-temporal. The flattened dorsal surface of the post-temporal is ornamented with raised bony tubercles.

The supracleithrum is expanded and overlaps the upper end of the cleithrum. The lateral face of the supracleithrum is ornamented with a few weak ridges. The cleithrum is sigmoid in shape with its anterior edge produced medially. The endoskeletal girdle attaches to the internal face of the cleithrum.

The scapula contacts the cleithrum laterally, the coracoid ventrally and the mesocoracoid antero-medially. A large scapular foramen perforates the centre of the bone. Postero-dorsally the scapula has a prominent facet with which the anterior fin ray articulated. The remainder of the posterior edge is grooved. The coracoid is much larger than the scapula and considerably expanded antero-ventrally.

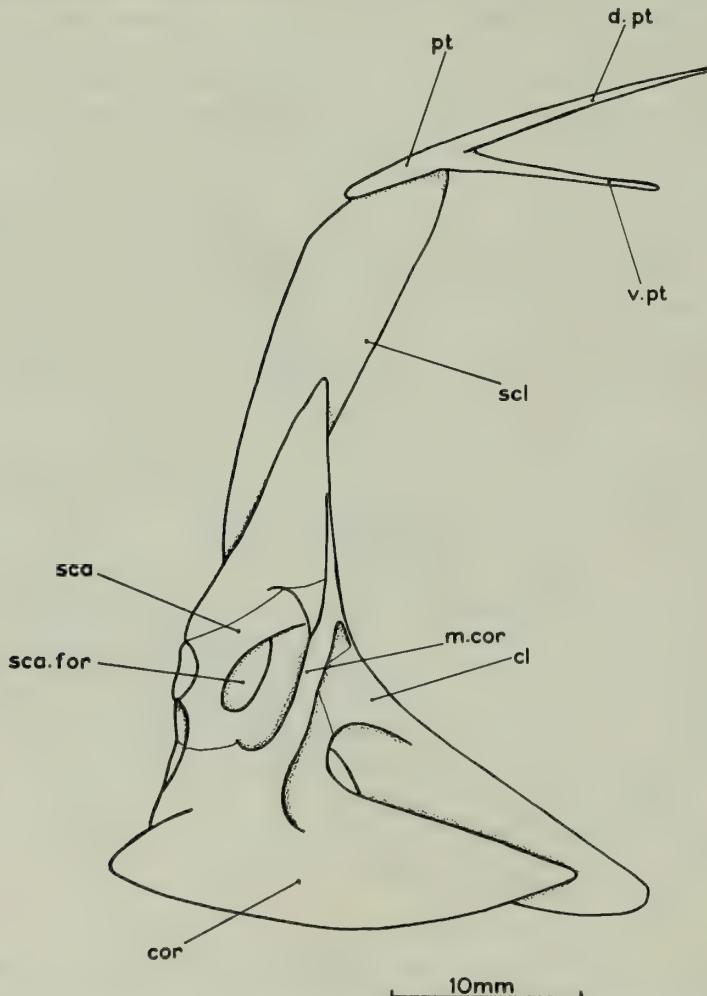


FIG. 62. *Halec eupterygius* (Dixon). Pectoral girdle of the left side in medial view.

The cleithrum and coracoid meet at their anterior extremities, leaving a fenestra between the two bones. Posteriorly the coracoid projects backwards below the fin insertion. The mesocoracoid arch is relatively narrow.

Vertebral column. The vertebral column consists of 45 vertebrae of which at least 20 and possibly as many as 22 are caudal. Each centrum is slightly longer than deep and is mesially constricted. The anteriormost neural arches are laterally compressed and expanded, not fused to the corresponding centra. More posteriorly the neural arches are more intimately connected to the centra. The precaudal vertebrae bear ventro-lateral transverse processes which support the pleural ribs. The ribs are long and narrow and decrease in size towards the end of the precaudal region. The first three or four caudal vertebrae have laterally flattened haemal arches without prominent spines. Haemal arches posterior to these are less expanded and are drawn out into backwardly curved haemal spines.

Halec haueri (Bassani)

(Text-figs. 63, 64)

- 1879 *Elopopsis haueri* Bassani : 164.
 1946 *Halec haueri* (Bassani) ; d'Erasmo : 90.
 d'Erasmo lists the earlier references.

DIAGNOSIS (emended). *Halec* species of standard length not exceeding 22 cm. Length of head with opercular apparatus greatly exceeds the maximum depth of the trunk, which is contained almost four times in the length from the pectoral arch to the base of the caudal fin. Length of the mandible exceeding the depth of the head at the occiput. Vertebrae 40 in number of which 18 are caudal. Dorsal fin with 13 or 14 rays, anal fin small and remote with 9 feeble rays.

HOLOTYPE. Almost complete but badly weathered specimen in the Geologische Bundesanstalt, Vienna, from the Lower Cenomanian of Lesina (= Hvar) in the Adriatic.

MATERIAL. The holotype and several further specimens in the Naturhistorisches Museum, Vienna. The major part of the description was obtained from a single excellent specimen, number 1902.11.5, in the Bayerische Staatssammlung für Paläontologie, Munich. All of the material is from the Lower Cenomanian of Lesina.

DESCRIPTION. *Skull.* The entire head region differs little from that of *Halec eupterygius* already described. The skull-roof is remarkably similar with the same arrangement of tubercular ornamentation, the enormous extent of the frontals, the unroofed post-temporal fossa and the prominent supraorbital bone. The jaw suspensorium is vertical with the quadrate condyle lying below the occiput as in *Halec eupterygius*. The dermal upper jaw is toothed, the maxilla bearing the characteristic forwardly inclined teeth at the posterior end.

Certain of the bones of the hyoid arch are shown whereas they were not preserved in *Halec eupterygius*. Both the ceratohyal and epihyal are long and shallow and

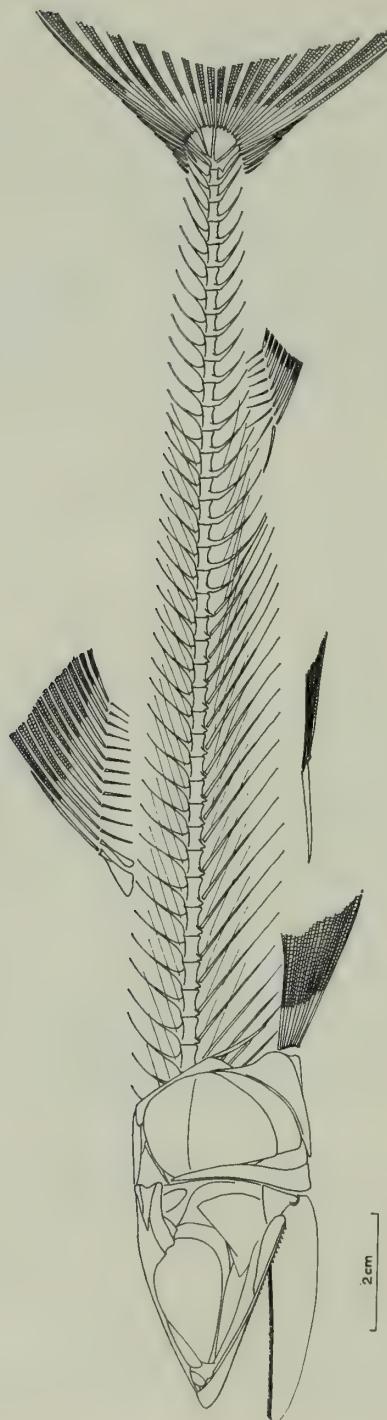


FIG. 63. *Halec haueri* (Bassani). Restoration of the skeleton, scales omitted.

support at least 15 branchiostegal rays. The first 8 rays are small and of uniform shape, the remaining 7 gradually increase in size until the terminal ones are large and flattened. The urohyal is long and formed of two laminae of bone connected dorsally.

Paired fins and girdles. The pectoral girdle is like that of *Halec eupterygius*, but in addition a large postcleithrum projects postero-ventrally from the lower end of the supracleithrum. Eleven or 12 rays make up the pectoral fin, the first is unbranched, stout and basally ornamented with small tubercles. The pelvic bones lie below the dorsal fin and the fins are as large as the pectorals, also consisting of approximately 11 rays. Most of the rays are branched and ornamented in their basal regions.

Vertebral column. The vertebral column is shown in the restoration of the entire skeleton in Text-figure 63. It consists of approximately 40 vertebrae, of which 18 are caudal. The centra are slightly longer than deep and mesially constricted. In the precaudal region the neural arches are easily displaced from the centra indicating the looseness of the attachment in life. Ventro-lateral transverse processes occur on the precaudal centra for the articulation of the long, thin, flattened ribs. The first two caudal vertebrae only possess haemal arches with which the ribs articulate. Both epineurals and epipleurals are present on the first 30 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 63. The dorsal fin consists of 13 or 14 rays and is just within the anterior half of the back. The first finray is short, stout and unbranched with ornamentation on

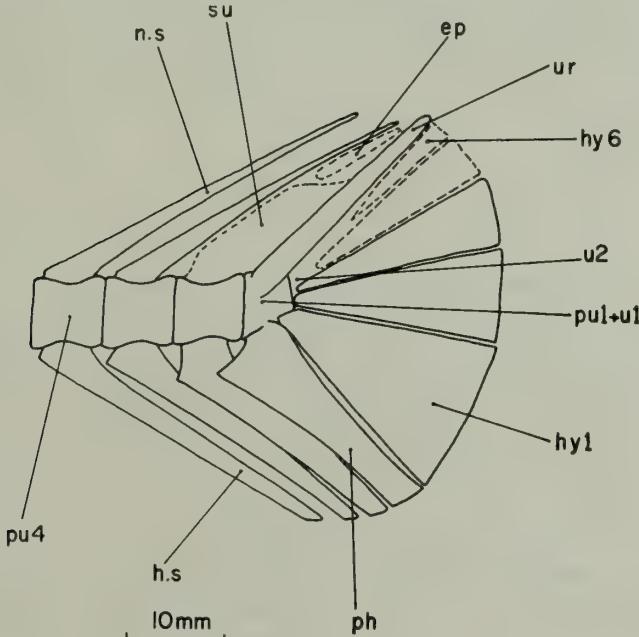


FIG. 64. *Halec haueri* (Bassani). Caudal fin skeleton in lateral view.

its basal region. The remaining rays are branched but unornamented. The anteriormost radial is expanded into a large anterior keel. The remainder of the radials are unexpanded.

The anal fin is small and remote with 9 feeble rays. The first ray is unbranched and unornamented and none of the radials is expanded.

The caudal skeleton (Text-fig. 64) is made up of six vertebrae, four preural vertebrae and two ural vertebrae. Preural vertebrae 3 and 4 bear normal neural and haemal spines, although the latter are somewhat expanded. The neural and haemal spines of these preural vertebrae support the accessory rays of the caudal fin. Preural vertebra 2 does not possess a neural spine, simply an expanded neural arch. Preural vertebra 1 and ural vertebra 1 are fused together to produce a compound centrum. The haemal spine of preural vertebra 1 (the parhypural), and the first two hypural elements articulate with the ventral edge of this compound centrum. Ural vertebra 2 is present as a small centrum supporting the hypurals of the upper lobe of the caudal fin, of which there are at least three. A large rod-like uroneural, inclined postero-dorsally, is associated with the dorso-lateral parts of both the ural vertebrae. The uroneural appears to be expanded anteriorly in the mid-line above the first preural vertebra, and is considered to be a stegural. A single epural is visible above the anterior expansion of the uroneural.

The caudal fin consists of 17 branched principal fin rays, together with at least 16 accessory fin rays.

Scales. The entire body is covered with a uniform coat of thin, minute scales. The scales along the course of the lateral line are enlarged and bear a posteriorly directed spine from the lateral face. The lateral line scales become progressively larger towards the caudal fin and on the caudal peduncle are irregular in shape with an enormous spine.

Genus **PHYLACTOCEPHALUS** Davis, 1887

DIAGNOSIS (emended). Halecidae in which the head is short but deepened; body also shortened and deepened. Jaw suspensorium vertical. Supraorbital absent. Approximately 10 branchiostegal rays. Vertebrae 32 in number. Dorsal fin in second quarter of the back. Pelvics sub-thoracic, larger than pectorals. Epineurals on the first 19 vertebrae. Complete covering of minute scales, enlarged along the lateral line.

TYPE SPECIES. *Phylactocephalus microlepis* Davis.

REMARKS. This genus was erected by Davis (1887) but subsequently Woodward (1901 : 218) synonymised it with *Halec*. There are sufficient differences to warrant separation into two distinct genera and the original generic name of *Phylactocephalus* is re-erected.

Phylactocephalus microlepis Davis

(Text-figs. 65, 66)

- 1887 *Phylactocephalus microlepis* Davis : 605, pl. 35, fig. 2.
 1901 *Halec microlepis* (Davis) Woodward : 218.

DIAGNOSIS (emended). *Phylactocephalus* of standard length not exceeding 18 cm. Length of the head with the opercular apparatus just exceeds the maximum depth of the trunk. Length of the mandible equivalent to the depth of the head at the occiput. Vertebrae 32 in number of which 16 are caudal. Dorsal fin with 17 rays occupying the second quarter of the back. Anal fin small and remote with 11 rays.

HOLOTYPE. Specimen number P.4757 in the B.M.N.H., a complete but flattened fish from the Middle Cenomanian of Hajula, Lebanon.

MATERIAL. Holotype and several other specimens in the B.M.N.H., numbers P.105, P.46453, P.47318 from the Middle Cenomanian of Hakel ; P.47329 from the Middle Cenomanian of Hajula, Lebanon.

REMARKS. The type specimen was initially poorly described by Davis (1887 : 605, pl. 35, fig. 2). His description was later corrected by Woodward (1901 : 218) when he transferred the species to the genus *Halec*. The type specimen was developed in acetic acid by the transfer method together with a complete, exceptionally well preserved specimen, number P.105. Since all the material is flattened, neurocranial description is difficult, however the postero-lateral region of the skull-roof is partially shown in specimen number P.47318.

DESCRIPTION. *Neurocranium.* The majority of the skull-roof is formed from the enlarged frontals which extend posteriorly almost to the occipital border. Laterally the frontal is curved above the orbital region to overlap the dorsal surface of the sphenotic and form the hind end of the orbit. Postero-laterally the frontal is deeply indented, and this marks the anterior extent of the unroofed post-temporal fossa. The frontals are uniformly ornamented with minute bony tubercles. In the snout region the frontals curve antero-ventrally. The sphenotic projects from beneath the frontal at the rear end of the orbit. The pterotic forms the postero-lateral border to the neurocranial roof, contacting the frontal and parietal medially. The dorsal surface of the pterotic has a prominent longitudinal crest which separates the post-temporal fossa from the dilatator fossa. The crest has a small posterior foramen which transmitted the lateral line canal into the pterotic. Ventro-laterally the pterotic has an elongated groove and this represents the hind region of the hyomandibular facet. Anteriorly the hyomandibular facet is cup-shaped and formed of sphenotic and prootic.

Within the orbit the parasphenoid is slightly curved and possesses small ventro-laterally inclined flanges. Towards the snout the parasphenoid flattens where it contacts the vomer. The vomer appears to contact the underside of the mesethmoid anteriorly and has slight lateral extensions which parallel those of the mesethmoid.

Hyopalatine bones. The hyomandibular is large and has a double head. The posterior part of the head is elongate and lies in a horizontal plane but the anterior

part is short and inclined antero-ventrally. The opercular process is pronounced and in the upper half of the bone. The lateral face of the hyomandibular bears a prominent crest running from the anterior head region back to the posterior edge. In front of the crest the hyomandibular is thin and tapers ventrally, this region is covered laterally by the metapterygoid.

The quadrate is a stout triangular bone with a transversely arranged condyle. Postero-dorsally the upper edge is excavated. This indentation marks the upper region of the groove on the medial face of the quadrate which housed the symplectic. The symplectic is narrow and inclined forwards ventrally. The posterior edge of the quadrate is thickened. Dorsally the quadrate contacts the metapterygoid and anteriorly attaches to the postero-medial region of the ectopterygoid.

The metapterygoid is a flattened membranous bone overlapping the anterior extent of the hyomandibular. Laterally on the metapterygoid a shallow crest passes obliquely backwards. More dorsally this crest marks the anterior edge of the metapterygoid. Anteriorly the metapterygoid contacts the postero-dorsal part of the ectopterygoid.

The ectopterygoid is elongate and bent through a slight angle near to its posterior end. Anteriorly the ectopterygoid meets the palatine in an elongate suture. A single row of teeth is present on the ectopterygoid, and these are acutely pointed, laterally compressed and evenly spaced. The teeth decrease in length towards the posterior region, where they are inclined slightly forwards. The teeth are finely striated, unexpanded basally and firmly fused to the bone. The tooth row is continuous on to the palatine. As well as the marginal row of teeth the palatine has an inner row of longer, more needle-like teeth. The palatine is supported by the lateral ethmoid dorsally. This latter bone is expanded above the dorso-medial surface of the palatine and firmly attached to it. Anteriorly the palatine articulates with the lateral edge of the vomer. The palatine has a small dorso-lateral maxillary process near its anterior end. This process is excavated terminally, and was filled and capped by cartilage in life.

Dermal upper jaw. The premaxilla is elongate and makes up the anterior half of the oral border of the upper jaw. Anteriorly the premaxilla is deepened and wrapped around the snout. The lateral face is ornamented with a large number of minute tubercles. The premaxilla tapers posteriorly and lies ventral to the maxilla. The dorsal edge of the premaxilla is inserted into a shallow groove on the ventro-lateral region of the maxilla. A fringe of small pointed teeth is present on the oral border of the premaxilla.

The maxilla is long and thin with an expanded and medially inclined head. The facet on the maxilla which housed the maxillary process of the palatine is small and bounded fore and aft by small bony projections. A marginal tooth row is continuous with that on the premaxilla, but posteriorly the teeth are lengthened and inclined forwards.

Above the posterior end of the maxilla is a conspicuous supramaxilla which narrows anteriorly but is deeper posteriorly where it extends beyond the end of the maxilla. The supramaxilla is ornamented with minute tubercles.

Mandible. The dentary forms the major part of the mandible and has a V-shaped posterior indentation. The symphysial region is considerably constricted but posteriorly the dentary is deep. The oral border supports a dense cluster of small acutely pointed teeth. Whether these teeth were arranged in definite rows could not be ascertained, although there is a distinct row of minute conical teeth on the extreme oral edge. This marginal row of teeth resembles that on the dermal upper jaw, whereas the more internal teeth are similar to those on the palato-pterygoid.

The articular forms the posterior part of the mandible and has a shallow, transversely orientated facet. On the postero-lateral surface a small pore, just below and behind the articular facet, transmitted the mandibular sensory canal. The sensory canal ran within the articular and opened into a deep groove anteriorly. This groove is continued on the ventro-lateral part of the dentary. Along much of its length on the dentary the groove is covered by a dorsal flange of bone.

The lateral surface of the mandible is ornamented with minute tubercles. Above the sensory canal groove the tubercles radiate backwards from the symphysis, but below the groove the tubercles are much less prominent and regular. The articular ornamentation is confined to the region below the articular facet.

The angular is a small knob of bone attached to the postero-ventral region of the articular and is strongly ornamented with bony tubercles.

Opercular bones. The preoperculum is deep and narrow and vertical in position. Dorsally the preoperculum ends below the upper limit of the hyomandibular. The anterior edge of the preoperculum lies against the posterior face of the crest on the hyomandibular and ventrally abuts against the posterior edge of the quadrate. The ventral extremity of the preoperculum is slightly broadened. The preopercular sensory canal ran within a groove in the upper half of the bone, but in a definite tube more ventrally. This tube opens anteriorly at the lowermost extremity of the preoperculum beneath the quadrate condyle. The lateral face of the preoperculum is liberally ornamented with minute tubercles.

The operculum has a straight, vertical anterior edge and the opercular facet occurs approximately one-third of the way down. Dorsally and posteriorly the operculum is rounded, but ventrally the edge is obliquely inclined. From the articulatory facet a horizontal strengthening ridge extends back across the inner face of the operculum. The operculum is ornamented with bony tubercles which radiate from the region of the opercular facet. The tubercles are absent from a narrow region anteriorly and antero-dorsally.

The suboperculum is large and deep with its dorsal edge lying medial to the operculum. From the antero-dorsal region of the suboperculum a small projection extends dorsally. The whole anterior edge of the suboperculum is thickened but the remainder, like the operculum, is thin. Externally the characteristic tubercles are arranged randomly.

A small, ornamented interoperculum is present beneath the ventral extremity of the preoperculum and suboperculum.

Hyoid arch and branchiostegal rays. Separate dorsal and ventral hypohyals are attached to the anterior end of the shallow, elongate ceratohyal. The epihyal, like the ceratohyal, is long and shallow. Both ceratohyal and epihyal bear branchiostegal rays ventrally. The number of branchiostegal rays is approximately 10 and these become progressively stouter posteriorly. The urohyal is elongate and formed of two narrow lamellae of bone which contact each other along their dorsal edges. The urohyal extends back to the level of the articular facet of the mandible.

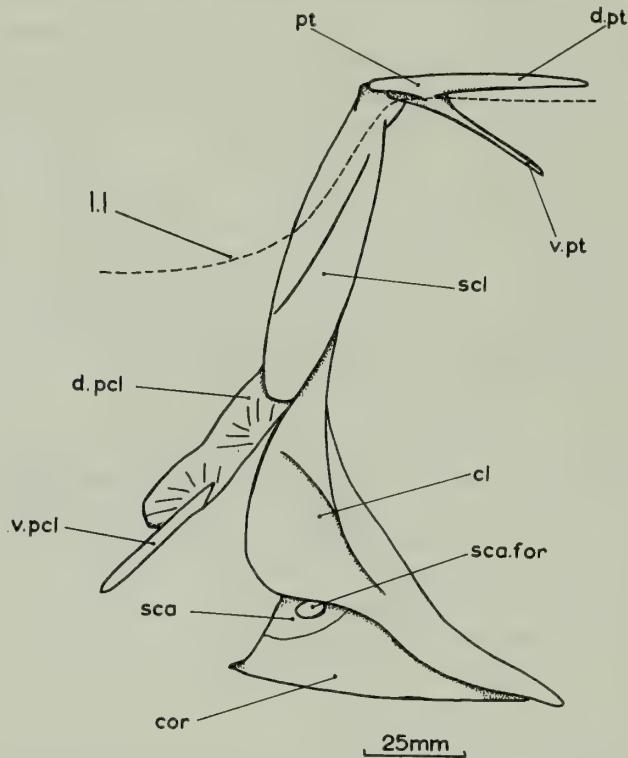


FIG. 65. *Phylactocephalus microlepis* Davis. Pectoral girdle of the right side in lateral view.

Pectoral girdle and fin. The pectoral girdle is shown in lateral view in Text-figure 65. The post-temporal has a flattened, oval, dorsal limb articulating with the epiotic, and a shorter, strut-like ventral limb articulating lower down on the posterior face of the neurocranium. Posteriorly the post-temporal is expanded to provide a medial facet for the articulation of the supracleithrum. The dorsal surface of the upper limb of the post-temporal is ornamented with minute tubercles and the lateral line sensory canal passed through the main body of the bone.

The supracleithrum is laterally flattened, with a thickened anterior edge. It is ornamented with minute tubercles arranged in rows following the long axis of the bone. The lateral line canal entered the supracleithrum midway down its posterior

edge. Ventrally the supracleithrum attaches to the lateral face of the upper region of the cleithrum.

The dorsal postcleithrum is similar in form to the supracleithrum, with a thickened anterior edge. The ornamentation of tubercles on the lateral face of the dorsal postcleithrum is from two distinct areas and the posterior edge of the bone is indented near its mid-point. (This seems to indicate that the dorsal postcleithrum represents the fusion of two separate elements.) The ventral postcleithrum is a small flattened rod of bone attached to the antero-ventral part of the dorsal postcleithrum.

The cleithrum is large and curved with its anterior edge inclined medially. Dorsally the cleithrum is narrow but more ventrally it expands where it follows the contour of the edge of the suboperculum. The anterior termination of the cleithrum is medial to the lowermost extremity of the preoperculum. The cleithrum is ornamented with radiating rows of tubercles.

The endoskeletal girdle attaches to the internal face of the cleithrum and projects posteriorly and medially. The posterior edge of the scapula is thickened and has a distinct saddle-shaped facet for the anterior fin ray. The coracoid is larger and curves forwards ventrally to contact the anterior extremity of the cleithrum. A strengthening ridge from the scapulocoracoid junction passes forwards along the dorsal surface of the anterior extension of the coracoid. The coracoid projects posteriorly below the fin insertion.

The pectoral fin has approximately 12 rays, the first ray being unbranched. All of the rays are stout basally and some are ornamented with bony tubercles. The fin is inserted low on the flank.

Pelvic girdle and fin. Each pelvic bone is stout, flattened and with a prominent vertical strengthening ridge running along its length. The bones taper anteriorly to contact each other at the extremities. The posterior regions are thickened to form a prominent articulatory region for the fin rays and unite in the mid-line.

The pelvic fin consists of approximately 11 rays and the first ray is unbranched. As in the pectoral fin the rays are stout, and certain of them are ornamented with ridges and tubercles. The rays are exceedingly elongate, the fin itself being much larger than the pectoral. The pelvic fins are in a sub-thoracic position, but the girdle does not contact either the cleithrum or the postcleithrum.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 66. It has approximately 32 vertebrae, of which 16 are caudal. The individual centra are slightly longer than deep and are mesially constricted. The anterior neural arches are not intimately connected with the centra but the more posterior arches have a much closer connection, although the suture between the two structures is always clearly visible. In the precaudal region paired ventro-lateral transverse processes are found on each centrum and associated with these are long, thin, flattened pleural ribs. The first two caudal vertebrae bear haemal arches but only rudimentary haemal spines. More posteriorly the haemal spines are fully formed. Epineurals and epipleurals are present on the first 23 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 66. The dorsal fin has 17 stout rays, and occupies the second quarter of the back. The first ray is shorter than the subsequent ones and unbranched, with its basal region ornamented. The remainder of the rays are branched and supported by elongate proximal radials. The anteriormost proximal radial is expanded anteriorly into a large keel-like structure. Traces of the medial radials are visible extending between the bases of adjacent fin rays.

The small anal fin consists of 11 feeble rays and is remote in position. The first ray is short and unbranched, the remainder are all branched. None of the proximal radials is expanded.

The caudal fin is supported by four or five centra. Three of the centra are free preural centra, the first preural vertebra appearing to be fused with the centrum of ural vertebra 1. Ural vertebra 2 may be present as a terminal half-centrum. The remainder of the caudal skeleton is indeterminable.

The fin itself is composed of 17 branched principal rays, and approximately 16 accessory rays.

Scales. The entire body is covered with a uniform coat of small scales, regular in shape and arrangement and closely packed. The scales are not present on the opercular bones but do cover most of the cheek region. Each scale bears a minute, longitudinal crest and these crests are continuous, producing a regular longitudinal series of parallel ridges along the body. The scales along the course of the lateral line are enlarged and thickened with the longitudinal crests becoming much more pronounced towards the caudal peduncle. On the peduncle the crests fuse with one another to produce a lateral, longitudinal flange.

Genus **HEMISAURIDA** Kner, 1867

DIAGNOSIS (emended). Halecidae in which the head is not deepened but slightly elongated; body shallow and not elongated. Supraorbital absent. Jaw suspensorium inclined anteriorly. Preoperculum with a greatly extended posterior spine. 16 branchiostegal rays. Dorsal fin in the second quarter of the back. Pelvics abdominal but smaller than the considerably elongated pectorals. Epineurals on the first 23 vertebrae. Body completely naked.

TYPE SPECIES. *Hemisaurida neocomiensis* Kner.

REMARKS. The genus was erected by Kner in 1867 to contain the single species *Hemisaurida neocomiensis*. The holotype of this species is a fragment of the head in the Geologische Bundesanstalt, Vienna. The specimen is from the Lower Cenomanian, Comen, near Trieste. A more complete specimen of this species, lacking the tail region and the tip of the snout is also present in Vienna. These are the only specimens of the type species and both were examined.

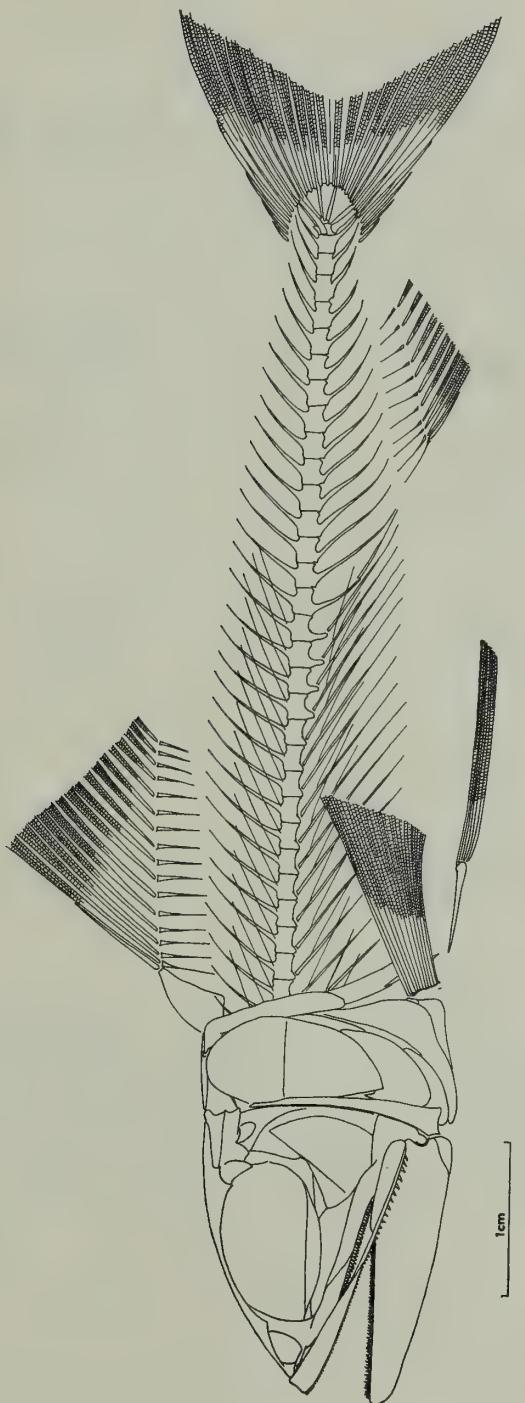


FIG. 66. *Phylactocephalus microlepis* Davis. Restoration of the skeleton, scales omitted.

Hemisaurida hakelensis sp. nov.

(Text-figs. 67-69)

DIAGNOSIS. *Hemisaurida* of standard length up to 5·5 cm. Length of the head with the opercular apparatus two and a half times the maximum depth of the head, and equal to just under half the length from the pectoral arch to the base of the caudal fin. Vertebrae 35 in number of which 17 are caudal. Dorsal fin in the second quarter of the back with 11 rays. Anal fin remote and consisting of 9 rays.

HOLOTYPE. B.M.N.H. number P.48777, a flattened fish from the Middle Cenomanian, Hakel, Lebanon.

MATERIAL. The holotype and specimen numbers P.48778, P.48779, P.48780 in the B.M.N.H., from the Middle Cenomanian of Hakel, Lebanon.

DESCRIPTION. *Neurocranium*. The neurocranium is somewhat elongate, shallow and with a large orbital region. The orbit is bordered dorsally by the frontal and limited anteriorly by a prominent lateral ethmoid. At the hind end of the orbit, the frontal extends laterally above the sphenotic. The sphenotic passes ventro-medially to contact the prootic within the anterior portion of the hyomandibular facet. The prootic forms part of the lateral wall of the cranial cavity and both the anterior and posterior openings of the trigemino-facialis chamber can be seen in it. The openings are separated by a strut of the prootic. Ventrally the prootic contacts the ascending process of the parasphenoid. At the base of the ascending process is a notch in the anterior edge marking the passage of the efferent pseudobranchial artery. Posterior to this notch, still in the parasphenoid, is a forwardly directed foramen which transmitted the internal carotid artery. The parasphenoid, in the base of the orbit, bears lateral flanges.

Hyopalatine bones. The hyomandibular is a shallow bone with an elongated head. The anterior region of the head fits into the cup-shaped facet formed from the sphenotic and prootic, whilst the posterior region fits into an elongated facet within the pterotic. A prominent lateral crest, from the anterior head region, passes postero-ventrally to the rear edge of the hyomandibular in the vicinity of the opercular process. The crest passes ventrally along the rear edge of the bone and disappears at the ventral extremity. A second crest passes ventrally from the posterior head region of the hyomandibular to contact the main crest where the latter meets the posterior edge of the bone. The hyomandibular curves strongly forwards ventrally (Text-fig. 67). The anterior part of the hyomandibular is thin and laminate and overlapped by the prominent metapterygoid. This latter bone supports an oblique crest and is relatively large, with rounded posterior and dorsal edges. The ventral edge is straighter and contacts the dorsal edge of the quadrate. The quadrate is large and triangular with a prominent condyle. The rear edge of the quadrate forms a continuation of the forward curvature of the ventral hyomandibular region. The quadrate condyle thus lies beneath the rear end of the orbit. The ectopterygoid and the palatine form a continuous strut of bone ascending gradually from the quadrate. The suture between the two bones is below the extreme anterior orbital region. The endopterygoid is thin and attached to the

ERRATUM

p. 148. Under HOLOTYPE delete all and replace by:

American University, Beirut, number 104710, 104786, a complete fish in counterpart from the Middle Cenomanian, Hakel, Lebanon.

under MATERIAL delete all and replace by:

The holotype and another specimen in counterpart, American University, Beirut, number 106805, 106819, from the Middle Cenomanian of Hajula, Lebanon.

medial edge of the ectopterygoid, lying in the roof of the mouth associated with the ventro-lateral flange of the parasphenoid. Anteriorly the palatine articulation with the mesethmod region of the skull is unexpanded. The lateral ethmoid contacts the postero-dorsal surface of the palatine. The palato-pterygoid bar bears a continuous, single series of teeth along its entire length.

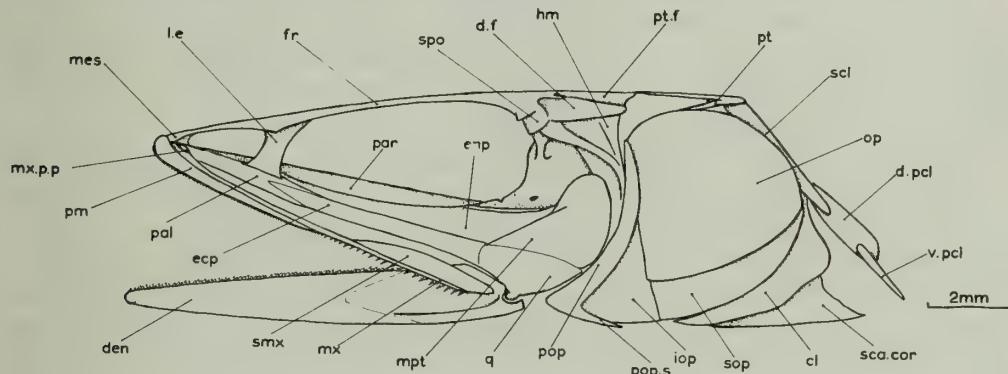


FIG. 67. *Hemisaurida hakelensis* sp. nov. Restoration of the skull in lateral view.

Dermal upper Jaw. The dermal upper jaw is shown in lateral view in Text-figure 67. The premaxilla is elongate and very shallow with no ascending process. Anteriorly the premaxilla is slightly expanded and wrapped around the snout. The premaxilla forms approximately the anterior half of the oral border of the upper jaw, and supports a fringe of minute teeth. The maxilla is almost twice as long as the premaxilla and is narrow along its entire length. It enters the oral border of the jaw behind the premaxilla and bears teeth on its ventral edge. The maxillary teeth are more prominent than those on the premaxilla and increase in size posteriorly, where they are forwardly inclined. At its extreme anterior end the head of the maxilla curves in towards the mid-line and bears a medial facet which is associated with the dorsal palatine surface. Above the maxilla is a long, low supramaxilla which just extends beyond the posterior end of the maxilla.

Mandible. The mandible is shown in lateral view in Text-figure 67. It is long, shallow and formed mostly of dentary. The articular facet is shallow and not well demarcated and there is no retroarticular process. The lateral face of the articular has a flange passing forwards horizontally from the articular facet. The groove and shelf produced above this flange support the maxilla and supramaxilla when the jaws are closed. The oral margin of the dentary has a series of small, clustered teeth.

Opercular bones. The opercular bones are shown in lateral view in Text-figure 67. The preoperculum is deep and narrow and curves forwards ventrally. Postero-ventrally it is produced into a prominent acutely pointed spine. The tube which contained the preopercular sensory canal traverses the entire length of the preoperculum and opens ventrally behind the condyle. The operculum is a very large

bone, as long as deep, with a rounded posterior edge. The suboperculum is reduced in extent and the interoperculum is small.

Hyoid arch and branchiostegal rays. Both the ceratohyal and the epihyal are visible below the dentary. Each is elongate and shallow, the ceratohyal attaching to a hypohyal anteriorly. The elongate median urohyal has an anterior articular region which is associated with the ventral region of the hypohyal. Sixteen branchiostegal rays are present, 8 of which articulate with the ceratohyal and 8 with the epihyal. The anteriormost 9 or 10 branchiostegal rays are uniform in length and thickness, but the remainder gradually increase in length and girth.

Paired fins and girdles. Due to the increase in size of the operculum the girdle has moved posteriorly and the occipital connection through the medium of the post-temporal is lengthened. Although the post-temporal is elongate it is of the normal forked nature with a more prominent flattened dorsal limb. The supracleithrum articulates with the postero-medial part of the post-temporal and from here it extends postero-ventrally to pass lateral to the upper part of the cleithrum. Two prominent postcleithra form a continuation of the supracleithrum. The dorsal postcleithrum is a large oval bone with a thickened anterior edge. The ventral postcleithrum is a thin splint of bone attached to the lowermost region of the upper. The lateral face of the cleithrum is expanded in a posterior direction above the fin insertion. The endoskeletal girdle is attached to the internal face of the cleithrum and the coracoid is visible ventrally as the more prominent of the two bones.

The pectoral fin is greatly elongated and composed of approximately 12 rays. The first ray is the largest and articulates directly with the posterior edge of the scapula. The first ray appears to be unbranched but the remainder gradually decrease in length and are all branched.

The pelvic bones are small slips of bone in the ventral body wall with posterior expanded articulatory regions. The pelvic fin consists of approximately 9 rays, the first of which is unbranched, the remainder branched.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 68. It is composed of 35 vertebrae, of which 17 are caudal. The centra are slightly longer than they are deep and mesially constricted. The last few caudal vertebrae decrease in length somewhat. The anteriormost neural spines are longer and more delicate than those on the caudal region. The anterior neural arches are not rigidly attached to the corresponding centra, but the posterior arches are more intimately attached. Each neural arch does not extend along the entire dorsal surface of the centrum but is confined more to the anterior end, this is much more noticeable in the caudal region where the neural arches and spines are larger. Prezygapophyses and postzygapophyses are present on every vertebra, but again are more pronounced in the caudal region. Small transverse processes are present on the ventro-lateral parts of the precaudal centra, and have well developed, long flattened pleural ribs articulating with them. The haemal arches gradually extend into haemal spines, a complete spine being present by the third caudal vertebra. Pleural ribs still

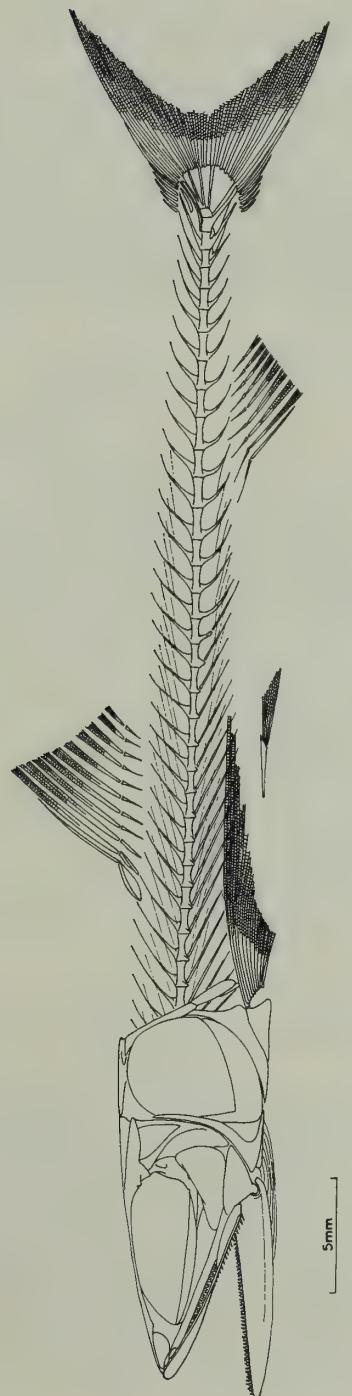


FIG. 68. *Hemisaurida hakelensis* sp. nov. Restoration of the skeleton.

5mm

associate with the haemal arches of caudal vertebrae 1 and 2. Both epineurals and epiplerals are associated with the first 23 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 68. The dorsal fin is short and deeper than long, positioned in the second quarter of the back. The fin has 12 rays, the first short and unbranched, the remainder longer and branched. All of the rays are segmented. The proximal radials are long and narrow except for the first which bears an expanded anterior keel.

The anal fin is remote and is made up of 8 or 9 small feeble rays. The first ray appears to be unbranched whilst the remainder are branched.

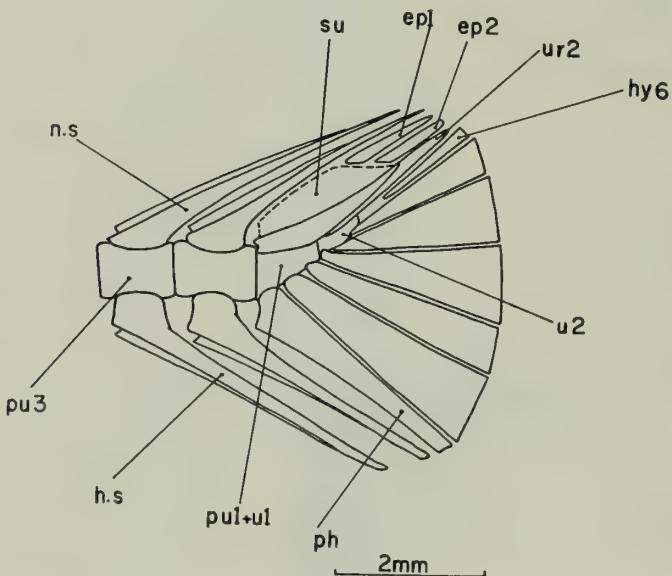


FIG. 69. *Hemisaurida hakelensis* sp. nov. Caudal fin skeleton in lateral view.

The caudal skeleton (Text-fig. 69) consists of five vertebrae, although one of these would seem to be a compound vertebra. Three free preural vertebrae are present (Preurals 2, 3 and 4), all possessing expanded haemal and neural spines. Preural vertebra 1 appears to have fused with ural vertebra 1 and this compound vertebra supports the parhypurals (haemal spine of preural 1), and two hypural elements, the first of which is the larger. The second ural vertebra is present as a terminal half-centrum associated with the hypurals to the upper lobe of the caudal fin. Two elongate, postero-dorsally directed, rod-like uroneurals are associated with the dorso-lateral regions of the compound centrum and the terminal half-centrum. One or two small epurals are present anterior to the uroneurals.

Order MYCTOPHIFORMES
Family **SARDINIOIDIDAE** nov.

DIAGNOSIS. Myctophiformes in which the post-temporal fossa is roofed ; the parietals meet in the mid-line anterior to the supraoccipital. Maxilla excluded from gape but expanded posteriorly with two supramaxillae. Premaxilla with long ascending process. Antorbital present, but no supraorbital. Both operculum and suboperculum large. Pelvics abdominal with a pelvic splint bone. Fulcral scales at base of tail. Vertebral elements incompletely fused. Ural vertebra 2 present as a terminal half-centrum. Scales cycloid or feebly ctenoid on body, also present on cheeks, operculum, skull-roof and posterior part of the maxilla.

Genus **SARDINIOIDES** von der Marck, 1858

- 1863 *Leptosomus* von der Marck : 49.
1940 *Cassandra* White and Moy-Thomas : 102.

DIAGNOSIS (emended). Sardiniodidae in which the body is short and somewhat deepened. Vertebrae between 30 and 32. Branchiostegals about 9 in number. Pleural ribs delicate. Dorsal fin in the front half of the back, with between 10 and 18 rays. Pectorals small and delicate, situated on the flank. Gap present between hypurals 2 and 3 and a corresponding gap between the fin ray bases. Scales ctenoid in larger species, cycloid in smaller ones.

TYPE SPECIES. *Sardinioides monasteri* (Agassiz).

REMARKS. Hay (1903 : 424) and Arambourg (1954 : 60) have maintained that the correct name of this genus is *Osmeroides* Agassiz, on the grounds that *Osmeroides monasteri* Agassiz is the type species of that genus. However the first publication of the name *Osmeroides* in a binomial was as *Osmeroides lewesiensis* (Agassiz 1837, 5 ; pls. 6ob, c), an elopoid fish in no way related to *Sardinioides*, thus preceding the first use of *Osmeroides monasteri* (Agassiz 1839, 5 ; pl. 6od). *Sardinioides* is therefore the valid generic name for the myctophiform fishes under consideration here.

***Sardinioides minimus* (Agassiz)**

(Text-figs. 70-72)

- 1839 *Clupea minima* Agassiz, 5 : 2 : pl. 61, fig. 1.
1844 *Clupea minima* Agassiz, 5 ; 2 : 120.
1866 *Clupea minima* Agassiz ; Pictet and Humbert : 65.
1901 *Leptosomus minimus* (Agassiz) Woodward : 246.
1903 *Osmeroides pontivagus* Hay : 424, pl. 33, figs. 1-4.

DIAGNOSIS (emended). *Sardinioides* of standard length not exceeding 45 mm. Length of head with opercular apparatus just less than one-third of the standard length, and equal to the maximum depth of the body. Pectoral fin with 14 rays ; pelvic fin with 9 rays. Dorsal fin with 11 rays ; anal fin with 9 rays. Four accessory radials in advance of the dorsal fin. Scales mainly cycloid, some feebly ctenoid.

HOLOTYPE. At one time in the Amic collection, Paris, but present whereabouts unknown. It was a flattened fish from the Middle Cenomanian of Hakel, Lebanon.

MATERIAL. Nine specimens in the B.M.N.H., 6 from the Middle Cenomanian of Hakel and 3 from the Middle Cenomanian of Hajula. All 9 specimens were prepared by the transfer method in acetic acid.

DESCRIPTION. *Neurocranium*. The neurocranium is shallow and reaches its maximum depth below the hind end of the orbit. The parasphenoid is long and straight. The frontals form the major part of the skull-roof and extend back to cover most of the cranial cavity. They meet in the mid-line in a sinuous suture and are widest at the hind end of the orbit where they extend above the dorsal surface of the sphenotic. In this region the frontal is indented. Within this indentation the dorsal surface of the sphenotic contacts the pterotic. The frontal meets the parietal and pterotic posteriorly and the sphenotic and pterotic laterally. The surface of all the bones is unornamented. The supraorbital sensory canal ran within the frontal above the orbit. Anteriorly the frontal tapers from in front of the orbit to insert on the dorsal surface of the broad mesethmoid region.

The parietales meet in the mid-line of the skull-roof and are rectangular in shape. They join the frontals anteriorly, the pterotics laterally in the roof of the post-temporal fossa and the epiotics posteriorly. The supratemporal lies on the posterior surface of the parietal.

The pterotic forms the postero-lateral region of the skull-roof, meeting the frontal and parietal medially in the roof of the post-temporal fossa, and the sphenotic anteriorly. The lateral surface of the pterotic is deeply excavated to form the dilatator fossa and the pterotic contacts the sphenotic in the anterior region of it. The hyomandibular facet is composed of sphenotic and pterotic with possibly an anterior contribution from the prootic. The otic branch of the infraorbital sensory canal passed within the pterotic above the dilatator fossa. The main infraorbital sensory canal from the last infraorbital bone connected with the otic branch on the dorsal sphenotic region, and then passed into the frontal.

In all of the specimens in which it is preserved, the last infraorbital remains closely attached to the dorsal sphenotic region (as it is in *Aulopus*, p. 208). Anteriorly the neurocranium is indistinct. The mesethmoid is a broad bone bifurcated anteriorly, producing two antero-lateral projections which are thickened and incline ventrally. The enlarged head of each maxilla fits beneath these projections, being retained in position by the vomer below. Ventro-lateral mesethmoid wings are also present associated with the palatine. A posterior process of the vomer passes back beneath the anterior end of the parasphenoid in the lateral ethmoid region. The lateral ethmoids attach to the parasphenoid and palatine ventrally.

A partially ossified interorbital septum may possibly represent an orbitosphenoid. Traces of a basisphenoid pedicel are also evident in the rear of the orbit.

Lying against the edge of the lateral ethmoid is a fragmentary bone which is probably an antorbital.

Hyopalatine bones. The hyomandibular is upright and narrow with a forwardly inclined, single and elongate head. A lateral crest on the anterior region of the head

passes postero-ventrally to the rear edge of the bone where it continues ventrally. At the point of contact with the posterior edge this lateral crest is produced into a small spine (Text-fig. 70). This spine lies lateral to the opercular process (approximately one-third of the way down the rear edge of the bone). The hyomandibular tapers ventrally and the symplectic is visible within an indentation of the upper edge of the quadrate. The quadrate is stout with a prominent transversely arranged condyle. The rear edge is thickened where it contacts the leading edge of the preoperculum. The palato-pterygoid bones were not shown well in any of the specimens examined, but they do not appear to differ to any extent from those of *Aulopus* described in the next section (Text-fig. 89, p. 211).

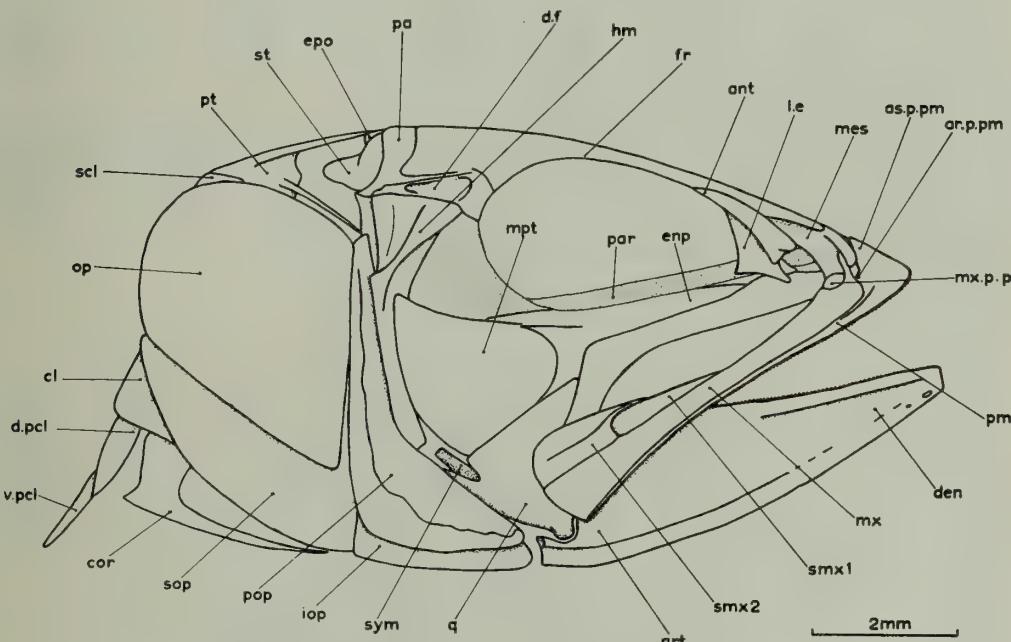


FIG. 70. *Sardiniodoides minimus* (Agassiz). Restoration of the skull in lateral view.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 70. The premaxilla completely excludes the maxilla from the oral border of the jaw. Anteriorly there is a prominent, broad ascending process but posteriorly the bone becomes long and very thin. The ascending process articulates with the anterior mesethmoid region. An articular process from the lateral region of the ascending process abuts against a facet on the anterior edge of the maxillary head. The alveolar arm of the premaxilla is closely applied to the ventral edge of the maxilla for its entire length.

The maxilla is larger and stouter than the premaxilla and has a medially inclined head. The antero-dorsal part has a depression into which the maxillary process of the palatine fits. This depression is bounded posteriorly by a flange. The

actual head of the maxilla, in front of this depression, is large and rounded and articulates with both the mesethmoid and the vomer. The maxilla becomes flattened and deepened and reaches its greatest depth posteriorly. On the dorsal edge of the maxilla are two reduced supramaxillae. The anterior is the smaller and is pointed in front; the posterior one has an antero-dorsal projection which lies along the dorsal edge of the anterior supramaxilla. All of the dermal upper jaw bones are smooth and unornamented.

Mandible. The mandible is shown in lateral view in Text-figure 70. It is long and deepened posteriorly. The dentary forms the greater part of both dorsal and ventral edges, as well as the lateral face. On the ventro-lateral part of the dentary is a deep groove covered by a dorsal flange. Anteriorly this groove is closed and opens to the exterior through one or two large pores. The groove and tube contained the mandibular sensory canal. The oral border of the dentary bears numerous small teeth.

The articular forms the posterior part of the jaw, with a transversely arranged, shallow articular facet. The posterior edge of the bone rises steeply from the facet to meet the dentary dorsally as the coronoid process. A small retroarticular process occurs behind the articular facet, and bears a lateral groove passing beneath the articular facet for the mandibular sensory canal.

The angular is a triangular knob of bone applied to the posterior end of the articular below the retroarticular process.

Opercular bones. The opercular bones are shown in lateral view in Text-figure 70. The operculum is large and deep with a straight, slightly thickened anterior edge, a rounded dorsal edge and an obliquely inclined ventral edge. The lateral face is unornamented and the opercular facet occurs near the upper limit of the anterior edge of the bone. The body scaling is continued on to the operculum. The suboperculum is also large and deep with its dorsal edge lying medial to the operculum. The bone is unornamented but the anterior edge is thickened and extended dorsally into a short process, medial to the operculum. The interoperculum is a prominent triangular bone lying medial to the ventral preopercular region. It is thin and unornamented and ends anteriorly just behind the retroarticular process.

The preoperculum inclines forwards ventrally where it is considerably broadened. It ends dorsally below the head of the hyomandibular, with its leading edge resting against the posterior crest of the hyomandibular. Below the hyomandibular crest, the anterior edge of the preoperculum is expanded into a slight convexity. In the extreme ventral region the leading edge of the preoperculum rests against the posterior edge of the quadrate. The preopercular sensory canal ran in a groove with a prominent overhanging flange. Body scaling extends onto the posterior regions of the preoperculum, but not on to this flange.

Pectoral girdle and fin. The supratemporal is never well preserved, but a projecting posterior portion appears to have housed a sensory canal. The post-temporal has a long curved dorsal limb articulating with the epiotic and an equally long ventral limb articulating with the posterior face of the neurocranium. The junction

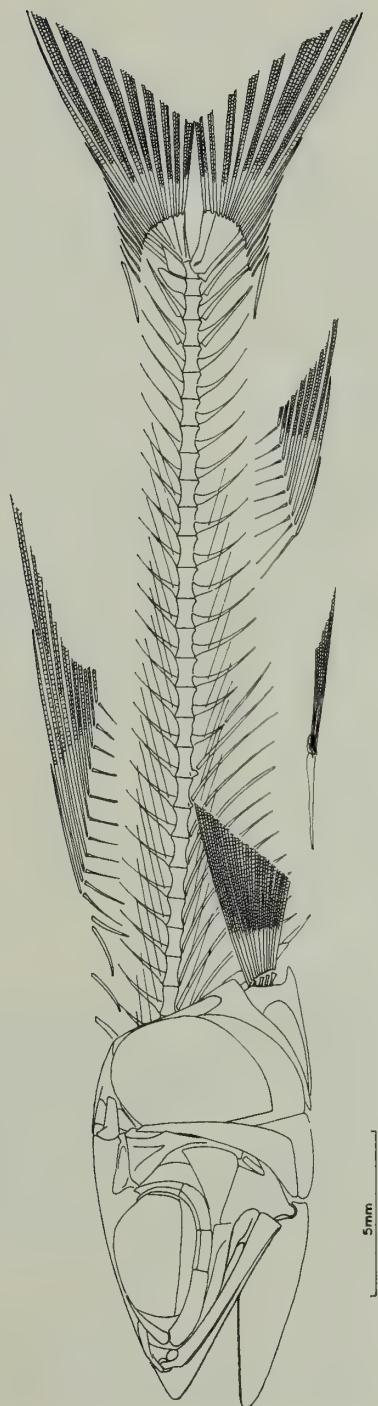


FIG. 71. *Sardinoides minimus* (Agassiz). Restoration of the skeleton, scales omitted.

of the two limbs is expanded and flattened vertically. The supracleithrum articulates with the postero-medial part of the post-temporal.

The supracleithrum is long and blade-shaped with a thickened anterior edge. The cleithrum is large and curved and expanded above the insertion of the fin. The endoskeletal girdle is attached to the internal face of the cleithrum, and the coracoid extends forwards to contact the cleithrum at the anterior end. Four pectoral fin radials support the fin rays and are slightly elongated and mesially constricted. Two postcleithra are attached to the rear edge of the cleithrum. The dorsal post-cleithrum is the larger, the ventral merely a narrow splint of bone.

The pectoral fin is composed of 14 rays, the first being the longest. All the rays are segmented and most of them, if not all, appear to be branched.

Pelvic girdle and fin. The triangular pelvic bones are sutured together in the mid-ventral line. Each is thickened posteriorly to form a prominent condyle supported by a thickened, lateral ridge. The pelvic fin has 9 rays, all of which are segmented, but several appear to have been unbranched. At the base of the fin is a small asymmetrically placed pelvic splint bone.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 71. It is composed of 30 vertebrae, of which 16 are caudal. The centra are slightly longer than deep and mesially constricted. The neural arches are not fused to the centra anteriorly, although the more posterior neural arches have a more intimate connection. The neural spines originate from the anterior end of each neural arch. The precaudal vertebrae bear very small transverse processes which elongate on the last three or four precaudal vertebrae. Long, curved, flattened pleural ribs articulate with the small transverse processes. The haemal arches are extended into prominent, curved haemal spines. Zygopophyses are present on both the dorsal and ventral surfaces of the vertebrae, but are most pronounced in the ventral caudal region. Epineurals and epipleurals are present on the first 20 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 71. The dorsal fin consists of 11 rays and is situated in the second quarter of the back. The second or third ray is the longest and much in excess of the basal length of the fin. The first ray is short and unbranched, the second is longer and also unbranched, although both are segmented. The subsequent rays are branched and segmented. The radials are long, flattened and unexpanded except in their articulatory head regions. Between the occiput and the origin of the dorsal fin, four accessory radials are present. The most anterior accessory radial is associated with the neural spine of the first vertebra. This association between accessory radial and neural spine may only have been ligamentous.

The anal fin is positioned behind the level of the rear of the dorsal fin and midway between the pelvics and the caudal. Nine rays are present in the anal fin; the first is short and unbranched although segmented, the second is long and unbranched, and the remainder of the rays are branched and segmented.

The caudal skeleton (Text-fig. 72) consists of seven vertebrae. Four free preural vertebrae are present. Preural vertebra 1 is fused with ural vertebra 1, and the second ural vertebra is present as a terminal half-centrum. Preural vertebrae 3, 4 and 5 bear slightly elongated neural and haemal spines which are somewhat expanded. Preural vertebra 2 (the first free preural vertebra) has an expanded haemal spine and no neural spine, but the neural arch is enlarged. The fused preural and ural vertebra bears the parhypural and the first two hypurals ventrally. Hypural 1 is larger than hypural 2, the latter not extending to the mid-line of the caudal fin. The second ural vertebra supports the upper four hypurals. The lower

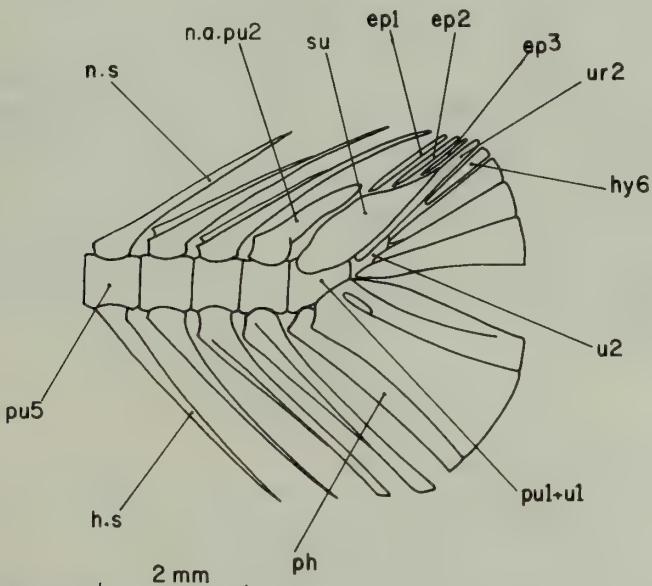


FIG. 72. *Sardinoides minimus* (Agassiz). Caudal fin skeleton in lateral view.

edge of hypural 3 does not reach the mid-line of the caudal fin, and thus there is a small gap left between the upper and lower hypural elements. The fused preural and ural centrum bears an enlarged, anteriorly expanded stegural. This is inclined postero-dorsally and a second uroneurals is present behind it. Three epurals associate with the dorsal edge of the anterior expansion of the stegural.

The caudal fin consists of 19 principal rays of which 17 are branched. Ten accessory rays occur epaxially and 10 hypaxially. In front of the anteriormost accessory ray, both dorsally and ventrally, is an enlarged fulcral scale.

Scales. The entire body is covered with cycloid scales which extend on to the opercular bones. Scales also cover the cheek region, the posterior end of the maxilla, the articular region of the mandible, and extend on to the dorsal surface of the skull as far as the centre of the orbit. In the smaller specimens the scales are strictly cycloid, but in larger specimens the scales may become very feebly ctenoid.

However, even on the larger specimens, not all the scales are ctenoid, those scales on or near the head are cycloid, the ctenoid scales being confined to the mid-body region.

Order CTENOTHRISSIFORMES

Family AUROLEPIDAE Patterson, 1964

DIAGNOSIS. See Patterson (1964 : 247), except that post-temporal fossa is occasionally roofed.

Genus *PATTERSONICHTHYS* nov.

DIAGNOSIS. Aulolepidae in which the post-temporal fossa is roofed. Length of the head greatly exceeds the depth of the trunk. Operculum devoid of scales. Vertebrae 30 in number of which 17 are caudal. Dorsal fin with 13 or 14 rays; anal fin behind rear of dorsal with 10 rays.

TYPE SPECIES. *Pattersonichthys delicatus*.

REMARKS. The genus *Pattersonichthys* is erected to contain several small specimens from Hajula, Lebanon. The generic name is dedicated to Dr. Colin Patterson of the B.M.N.H.

Pattersonichthys delicatus sp. nov.

(Text-figs. 73-77)

DIAGNOSIS. As for genus, only species.

HOLOTYPE. B.M.N.H. specimen number P.9976, a complete but flattened fish, from the Middle Cenomanian, Hajula, Lebanon.

MATERIAL. The holotype and two further specimens, P.9977a and P.9977b, also from the Middle Cenomanian, Hajula. All three specimens were prepared in acetic acid by the transfer method.

DESCRIPTION. *Neurocranium*. The neurocranium appears relatively shallow, and is deepest in the occipital region. The parasphenoid, visible in the base of the orbit, is straight. The frontals are flat, although the lateral edges curve down to form the dorsal margin of the orbits. The frontal tapers anteriorly to insert on to the dorsal surface of the mesethmoid and is unornamented. In the posterior region of the cranial cavity an incompletely roofed post-temporal fossa is present. The roof of the fossa has a curved indentation posteriorly. The frontal extends laterally above the dorsal surface of the sphenotic at the hind end of the orbit, and medially to cover the anterior half of the cranial cavity. Posteriorly the frontals contact the parietals and the pterotics. The pterotic makes up most of the postero-lateral edge of the neurocranium, meeting the sphenotic anteriorly and the frontal and parietal medially. The lateral faces of the pterotic and sphenotic are deeply excavated to form the dilatator fossa. The upper border of the fossa is delimited by a low crest on the pterotic passing backwards from beneath the frontal. The

hyomandibular facet is divided into two regions, an anterior cup-shaped concavity in the sphenotic and prootic, and a posterior elongated groove on the ventro-lateral surface of the pterotic.

The large parietals meet in the mid-line. The parietal contacts the frontal anteriorly and the pterotic laterally and enters into the composition of the roof of the post-temporal fossa. The remainder of the neurocranium is poorly shown. The epiotic appears to project posteriorly and the dorsal limb of the post-temporal bone is associated with its dorsal surface. In the region of the occipital condyle the exoccipital and basioccipital are thickened and meet in a prominent suture. Below the condylar region the parasphenoid is curved upwards slightly. In the base of the orbit the parasphenoid is expanded laterally into ventrally inclined flanges.

The mesethmoid is prominent but appears to have been only superficially ossified. It bears a pair of lateral wings inclined antero-ventrally, which are underlain by lateral extensions of the vomer. There is no connection laterally between the two bones. The palatine, antero-medially, is closely associated with the lateral edge of the vomer and also possibly the mesethmoid. The lateral ethmoids are not well ossified and ventrally contact the palatines. The lachrymal lies on the ventro-lateral region of the lateral ethmoid.

The articular head of the maxilla appears to have rested on the dorsal surface of the lateral part of the vomer and would thus also have contacted the ventral surface of the lateral wing of the mesethmoid. The posterior process or shaft of the vomer

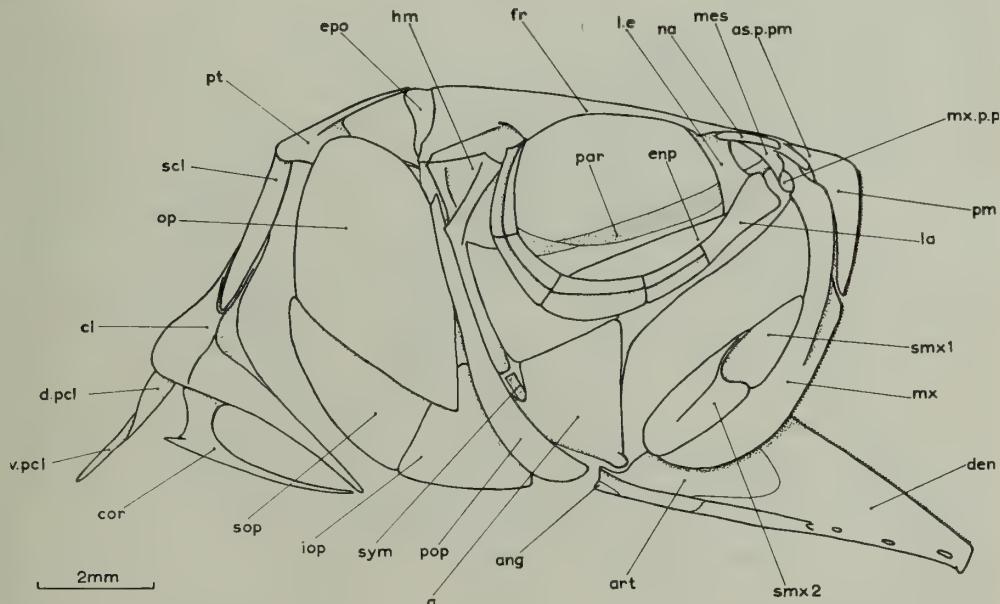


FIG. 73. *Pattersonichthys delicatus* gen. et sp. nov. Restoration of the skull of the holotype (B.M.N.H. number P.9976) in lateral view.

extends back beneath the anterior parasphenoid region. Whether the vomer is toothed could not be seen.

Within the postero-ventral region of the orbit there is a long basisphenoid pedicel, but no evidence of an orbitosphenoid could be seen. At the anterior end of the snout a small nasal bone lies lateral to the anterior region of the frontal and extends on to the dorsal surface of the mesethmoid.

Infraorbital bones. A circumorbital ring of bones is present although they are poorly preserved and fragmentary. There are five or six bones in the series, including the lachrymal. The bones are narrow and roughly equal in size except for the lachrymal which is larger. The bones are grooved laterally for the infraorbital sensory canal. The last infraorbital articulates with the sphenotic. Dorsal to the lachrymal is a further bone which probably represents an antorbital. The lachrymal and the first infraorbital show signs of having possessed a slight subocular shelf.

Hyopalatine bones. The hyomandibular is slender and vertical with a single articular head. The opercular process is small, in the upper third of the bone, and covered laterally by the preoperculum. Anteriorly the hyomandibular is thin but its posterior edge is considerably thickened. Just within the upper half of the posterior edge is a short process projecting postero-laterally from the crest which runs along the posterior edge of the bone. The hyomandibular tapers ventrally and a stout symplectic bone connected it with the quadrate. The symplectic is attached

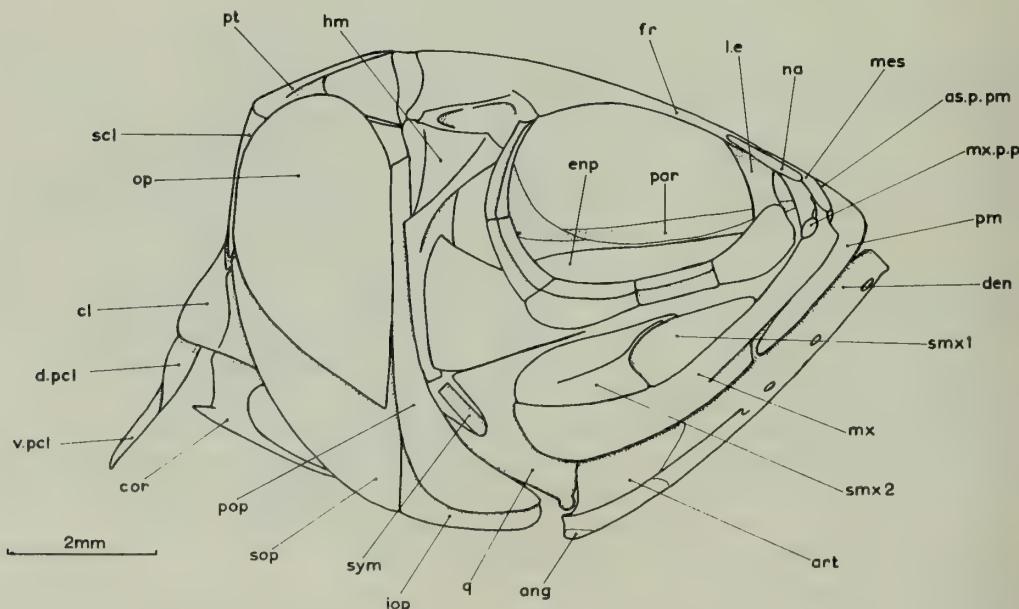


FIG. 74. *Pattersonichthys delicatus* gen. et sp. nov. Restoration of the skull in lateral view.
From B.M.N.H. number P.9977a.

to the medial face of the quadrate and inclines forwards at an angle to the hyomandibular. The quadrate is large and triangular with the anterior edge considerably longer than the posterior. The condyle is thickened and mesially constricted. The posterior edge of the quadrate is thicker where the preoperculum rests against it. The postero-dorsal edge of the quadrate is deeply excavated at the upper limit of the symplectic groove. The quadrate dorsally contacts the lower edge of the metapterygoid, and anteriorly the ectopterygoid. The remainder of the palate is not preserved, except anteriorly where the maxillary process of the palatine is visible. This process is in the form of a funnel-shaped protuberance from the dorso-lateral part of the palatine.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figures 73 and 74. It is long and extensively toothed. The premaxilla has a short, broad, ill-defined ascending process. Laterally the ascending process has a small articulatory process for a facet on the leading edge of the maxillary head. The posterior process of the premaxilla is prominent with a broad oral border covered by small recurved teeth. The premaxilla forms the anterior third of the oral border of the upper jaw. The external face of the premaxilla is unornamented.

The maxilla is also unornamented. Anteriorly the maxilla curves medially and has a large rounded dorso-medial depression, bounded posteriorly by a prominent flange. The maxillary process of the palatine is contained within this facet. Antero-medial to the facet the head of the maxilla is rounded. The maxillary head appears to be associated with the dorsal surface of the vomer and the undersurface of the mesethmoid. The anterior face of the maxilla, in front of the palatine facet, is excavated for the reception of the articular process of the premaxilla. The maxilla extends posteriorly above the premaxilla as a stout bar of bone. Behind the premaxilla the maxilla deepens, and the tooth-bearing margin is thinner and flatter although the stout part of the maxilla is continued back for some way above the dentigerous region. The toothed margin is a deep, curved flange ; the teeth are numerous anteriorly, but reduced in number towards the posterior end.

Two large supramaxillae are attached to the dorsal edge of the maxilla along most of its length. The anterior supramaxilla is a roughly oval slip of bone prolonged somewhat anteriorly. The posterior supramaxilla is larger and has a dorsal process extending anteriorly along the upper edge of the anterior supramaxilla. A ridge on this antero-dorsal process continues back on to the lateral face of the supramaxilla. Both bones are unornamented.

Mandible. The mandible is shown in lateral view in Text-figures 73 and 74. It is quite long and deep, with a pronounced coronoid process. The symphysis is blunt and not deepened, although there seems to be a slight ventral prolongation. The oral border of the dentary bears a group of small, clustered, recurved teeth. The mandibular sensory canal, in the dentary, ran within the bone, opening to the exterior through three or four prominent pores. The tube opens into a groove towards the posterior end of the dentary. The articular forms the posterior part of the mandible and the articular facet is shallow and transversely orientated. A small

insignificant retroarticular process occurs behind the facet and a groove on the lateral face of this process extends below the articular facet and passes forwards on the ventro-lateral surface of the articular. This groove carried the sensory canal. The posterior edge of the articular rises steeply from the facet to form the posterior part of the coronoid process. The angular is present as a small slip of bone applied to the postero-ventral region of the articular below the facet. The lateral face of the mandible is smooth and unornamented.

Opercular bones. The opercular bones are shown in lateral view in Text-figures 73 and 74. The preoperculum inclines forwards ventrally and dorsally ends just behind and below the head of the hyomandibular. The anterior edge of the preoperculum lies against the posterior face of the hyomandibular crest. Ventral to the hyomandibular, the anterior edge of the preoperculum is expanded into a small convexity. Below this slight expansion the preoperculum lies against the rear edge of the quadrate. The preopercular sensory canal ran in a deep groove, open posteriorly. A thin flange of bone overhangs this groove, neither the flange nor any other part of the bone is ornamented.

The operculum is deeper than long with a straight anterior edge which terminates in an acute point antero-ventrally. The ventral edge is obliquely inclined, whereas the rest of the margin is smoothly rounded. The opercular facet occurs just within the upper half of the bone and is supported by a horizontal strengthening ridge which passes across the inner face of the operculum. The lateral face of the operculum is unornamented.

The suboperculum is large with its dorsal edge lying medial to the operculum. It extends postero-dorsally for almost half of the depth of the operculum. The antero-dorsal corner of the suboperculum is produced into a small pointed process. The suboperculum is thin and delicate, except for a thickened anterior edge.

The interoperculum is a roughly triangular sheet of bone with a straight posterior edge which abuts against the anterior edge of the suboperculum. The interoperculum is thin and unornamented.

Hyoid arch and branchiostegal rays. The ceratohyal is large and rectangular in shape, with a deep lateral groove running along its length. The groove indicates the course of the hyoidean artery and is interrupted by an elongate fenestra approximately mid-way along the ceratohyal. There are two hypohyals. The exact number of branchiostegals is uncertain but they are arranged in two distinct groups. The ceratohyal supports several small, thin branchiostegal rays, possibly as many as five. The second group of rays arises from the epihyal and one from its junction with the ceratohyal. The branchiostegal rays on the epihyal are broad, long, flattened and four in number.

Pectoral girdle and fin. The pectoral girdle is shown in lateral view in Text-figure 75. The post-temporal has a long dorsal limb articulating with the epiotic and a shorter, thinner ventral limb passing antero-ventrally. The junction of the two limbs is somewhat flattened and expanded. No trace of a supratemporal could be found in any of the specimens.

The supracleithrum is stout and narrow and ventrally it articulates with the lateral face of the cleithrum, and is confined within a vertical groove. The cleithrum is a prominent sigmoid bone expanded lateral to the attachment of the endoskeletal girdle. The ventral part of the cleithrum curves forwards, and its anterior edge is bent medially.

The endoskeletal girdle is indistinct, although the thickened saddle-shaped facet on the postero-dorsal region of the scapula, with which the first fin ray articulated, is clearly defined. The coracoid has a long slender anterior process which curves forwards to the anteriormost tip of the cleithrum with which it connects. The ventral edge of the coracoid projects posteriorly as a short pointed spine below the fin insertion.

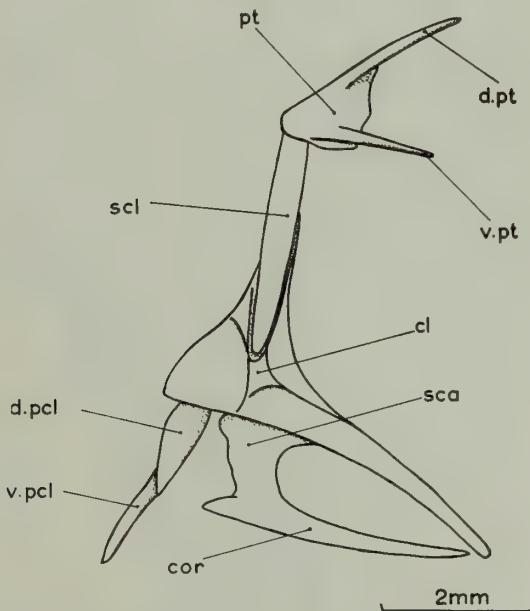


FIG. 75. *Pattersonichthys delicatus* gen. et sp. nov. Pectoral girdle of the right side in lateral view. From B.M.N.H. number P.9976.

The four radials articulate with the rear edge of the scapula, and the junction between the scapula and coracoid. Two prominent postcleithra are present; the larger dorsal one articulates with the medial face of the posterior expansion of the cleithrum, the ventral postcleithrum is smaller and joined to the upper postcleithrum dorsally and the pelvic bone ventrally.

The pectoral fin consists of 13 rays of which the first is the longest, the remainder decreasing in size. All of the rays are segmented distally, and most of them appear to be branched.

Pelvic girdle and fin. The pelvic bones are flattened, widest posteriorly and tapering to a point anteriorly. They contact each other in the mid-line in a long

suture. Although thin the pelvic bones are thickened somewhat posteriorly to form an articulatory condyle. A crest passes anteriorly along the lateral edge of the bone. The main body of the bone lies horizontally whereas the condyle is inclined obliquely. Medial to the condyle, the ventral postcleithrum is firmly attached. The anterior ends of the pelvic bones lie between the anterior coracoid processes.

The pelvic fin is long, prominent and composed of 8 rays. All the rays are segmented distally, and except for the first one or two are branched. The fin has a basal, asymmetrical, pelvic splint bone.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 76. It consists of 30 vertebrae, of which 17 are caudal. The centra are longer than deep, and mesially constricted. The neural arches are relatively stout but the spines are delicate. Each neural arch is confined to the anterior half of the corresponding centrum. The neural arches on the precaudal vertebrae are only loosely connected to the centra, but caudally the contact is much closer. Transverse processes only become evident on the posteriormost two or three precaudal vertebrae, and the pleural ribs on the remaining vertebrae articulate directly with the centra. Several of the most anterior precaudal vertebrae do not appear to possess pleural ribs. On the first caudal vertebra the haemal arch is not drawn out into a haemal spine, but on all the subsequent caudal vertebrae haemal spines are present. Zygapophyses are in evidence on the ventral regions of both precaudal and caudal vertebrae, whereas on the dorsal region of the vertebral column the zygapophyses are non-existent. Epineurals and epipleurals are present on the first 22 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 76. The dorsal fin is prominent and occurs in the second quarter of the back, consisting of 13 or 14 rays. The fifth ray is the longest and all the subsequent rays are segmented. The first four rays decrease in size anteriorly. The third and fourth rays are unbranched but segmented, but the first and second rays are neither branched nor segmented. The radials are long and narrow and unexpanded. The medial radials are visible between the bases of adjacent fin rays, as elongate constricted cylinders of bone inclined obliquely. In the region between the origin of the dorsal fin and the occiput three flattened accessory radials occur. The most anterior one is associated with the expanded neural spine of the first vertebra.

The anal fin is composed of 10 rays and arises just behind the rear of the dorsal fin. The third ray is the longest. It is greatly extended and both segmented and distally branched. The subsequent rays are all branched and decrease in size posteriorly. The second ray is shorter and segmented, the first is the shortest and spinous in form.

The caudal skeleton (Text-fig. 77) is composed of several vertebrae. Four preural vertebrae are present as separate units, the neural and haemal spines of these supporting the accessory rays of the caudal fin. The first preural vertebra is fused with the first ural vertebra. A free second ural vertebra is present as a small terminal half-centrum posteriorly. The haemal spines of the preural vertebrae are elongate, that of preural centrum 2 (the first free preural vertebra) is slightly flattened and expanded. The fused preural and ural vertebrae support the parhypural (the haemal spine of the first preural vertebra) and two hypurals. Postero-

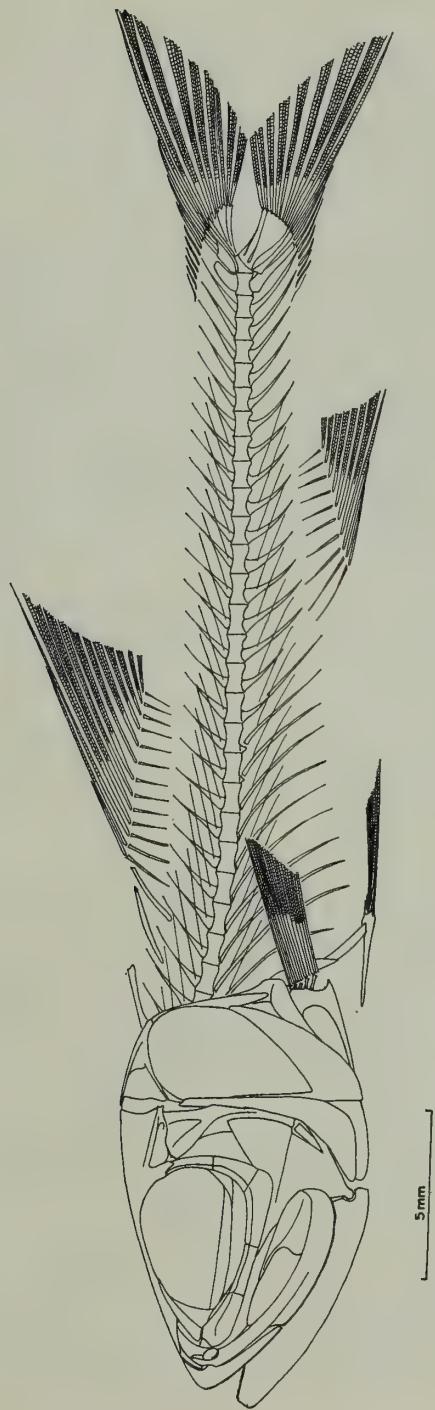


Fig. 76. *Pattersonichthys delicatus* gen. et sp. nov. Restoration of the skeleton, scales omitted.

dorsally the parhypural contacts the centrum by a narrow connection, and anteriorly overlaps the haemal spine of the second preural vertebra. The parhypural is long, narrow and flattened. The two hypural bones support the lower caudal lobe, hypural 1 is the larger. Hypural 2 is narrow and does not extend dorsally to the mid-line of the fin. The second ural vertebra supports the four hypurals of the upper caudal lobe. These hypurals have partially united to form a hypural plate which does not extend ventrally to the mid-line of the fin. There is thus a distinct gap in the mid-line of the caudal skeleton between the upper and lower hypural elements. Long, narrow neural spines occur on preural vertebrae 3, 4 and 5. The neural spine of preural vertebra 2 is missing and the neural arch is considerably expanded. Two uroneurals are associated with the dorsal surface of the terminal vertebrae. The stegural is formed from the anteriorly expanded first uroneural, and it is drawn out postero-dorsally. At least two, and possibly three, epurals are associated with the dorsal edge of the stegural.

The caudal fin has 19 principal rays, 17 of which are clearly branched. Nine accessory rays are present in front of the upper caudal lobe, and 9 below. The anteriormost accessory ray both above and below is slightly more flattened and more horizontally placed. This anterior ray may represent the remains of a fulcral scale.

Scales. The entire body is covered with small cycloid scales which do not appear to show any ctenoid tendencies. Scales are also present on the cheek region but not on the opercular bones.

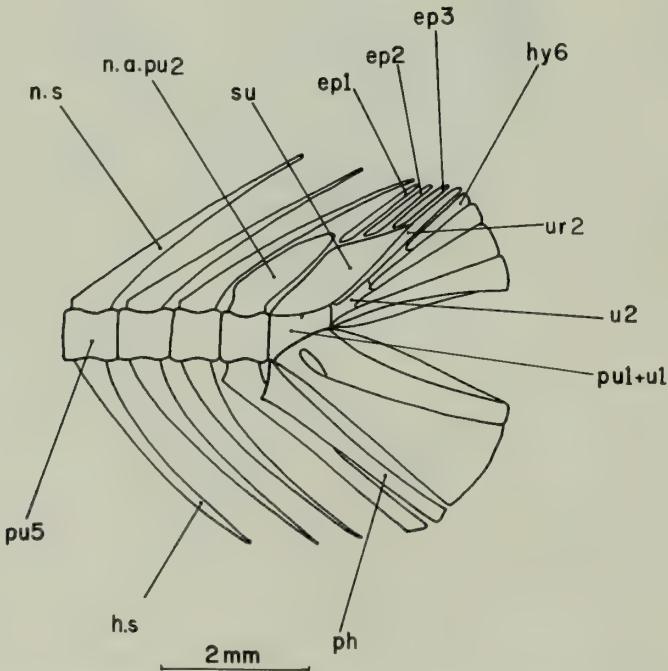


FIG. 77. *Pattersonichthys delicatus* gen. et sp. nov. Caudal fin skeleton in lateral view.

III. DISCUSSION

This section is devoted to a discussion of the new families and suborders erected in the systematic descriptions (Part II). Each group is considered separately.

Order SALMONIFORMES

(A) Suborder ICHTHYOTRINGOIDEI

A new suborder has been erected to contain the three genera *Ichthyotringa*, *Apateodus* and *Apateopholis* as set out in the systematic descriptions. The suborder has been divided into two separate but closely related families, the Ichthyotringidae and the new family Apateopholidae. Despite the similarities between the two (compare Text-figs. 3 and 15), the Apateopholidae is somewhat more advanced. The advanced characters form the basis of the familial division :—

ICHTHYOTRINGIDAE

1. Complete roof to the post-temporal fossa.
2. Supratemporal present but reduced.
3. Orbitosphenoid present.
4. Basisphenoid present.
5. Posterior infraorbitals expanded.
6. Jaw suspension vertical.
7. No cranial deepening.
8. Complete covering of cycloid scales.

APATEOPHOLIDAE

- | |
|---|
| Post-temporal fossa unroofed. |
| Supratemporal absent. |
| Orbitosphenoid absent. |
| Basisphenoid absent. |
| Infraorbitals much reduced in extent. |
| Jaw suspension forwardly inclined. |
| Cranium deepened. |
| Body naked except for a row of lateral line scales. |

Apart from these features the two families are linked by several primitive features of the body and tail, and by several advanced characteristics associated with the production of an elongate rostral region.

The rostrum is composed of premaxillae, maxillae, palatines, vomer and mesethmoid. In both families simplification has occurred by the loss of the nasals (or their combination with the mesethmoid) and the loss of both antorbital and supraorbital. Teeth are borne on the palatines and the premaxilla but not on the vomer. This rostral composition is similar to that seen in the dercetids (pp. 50–71) and certain of the 'alepisauroid myctophiforms' (Parr, 1929; Marshall, 1955).

The general form of the body is the same in both families and is short, relative to the rostral elongation, with approximately 40 vertebrae. The anterior neural spines are composed of separate lateral elements ; intermuscular bones occur along most of the column ; the dorsal fin is in the mid-region of the back ; the anal fin is remote ; the pelvics are abdominal, lying below the dorsal fin ; the pectoral fins are set low on the flanks and consist of a large number of rays. In addition to these features the caudal skeleton contains two free ural vertebrae, thus corres-

ponding to the condition seen in *Elops* (Nybelin, 1963) and some basal salmoniforms such as *Salmo* (Norden, 1961).

The Ichthyotringidae possess a complete covering of thin cycloid scales, whereas in the Apateopholidae the scales are confined to the lateral line only. This latter condition may indicate that some degree of stomach distensibility was possessed by *Apateopholis*.

The genus *Apateodus* is placed as an addendum (*incertae sedis*) to the family Ichthyotringidae. It is unfortunate that the genus is only known from skull material. The head appears to agree in certain features with that of *Ichthyotringa*, and is closer to this genus than to any other Cretaceous form so far described. Features shared by the two genera are as follows :

1. Parietals meet in the mid-line of the skull-roof.
2. Post-temporal fossa completely roofed.
3. Mesethmoid simple and pointed anteriorly.
4. Orbitosphenoid present.
5. Basisphenoid present.
6. Posterior infraorbitals greatly expanded, covering the hyomandibular and extending back to the preoperculum.
7. Rostral region from the same components, although in *Apateodus* it is considerably shorter.

The three genera placed in the suborder Ichthyotringoidei have not previously been associated together. The family Ichthyotringidae was first proposed by Jordan (1905) to include Cope's (1878) genus *Ichthyotringa*. Woodward (1901 : 265) placed the genus *Ichthyotringa* (*Rhinellus*) within his family Scopelidae among the Isospondyli. In the same work (1901 : 258) Woodward associated *Apateodus* with *Ichthyotringa*. Later, (1902 : 38) using more complete material, he put the genus *Apateodus* in the Enchodontidae. Regan (1911 : 120) considered *Apateodus* to be close to the genus *Alepisaurus* and concurred with Woodward's (1902) view that *Apateodus* belonged with the enchodonts. Kruizinga (1924) in his more extensive study of the head of *Apateodus* retained the genus within the enchodonts but related the family to the stomiatoids. Gregory (1933 : 204) mentioned *Apateodus* in connection with the enchodonts contained in his division Mesichthyes.

Jordan (1923 : 155) later placed the genus *Ichthyotringa* in the Myctophidae among the Iniomii, but Berg (1940 : 438) retained the familial name and it was contained in his order Scopeliformes. Bertin and Arambourg (1958 : 2272) placed the genus *Ichthyotringa* within the family Myctophidae of the suborder Myctophoidei.

Some mention of the historical aspect of the genus *Apateopholis* has already been given in the systematic description. The genus has not been considered by any author since Woodward (1901 : 232) placed it in the family Enchodontidae.

Neither *Apateodus* nor *Apateopholis* can be considered to be enchodonts (as constituted in this work) due primarily to the difference in palatine structure. The Enchontoidei are characterized by the presence of a single, terminal tooth on the palatine. Many other structures are also at variance with the enchontoids, for example the caudal skeleton and premaxillary arrangement.

Likewise *Ichthyotringa* cannot be retained in the myctophiform group (in which it has often been placed) because of the following characters :

1. Maxilla enters the gape behind the premaxilla and is toothed.
2. Premaxilla simple, with no ascending process.
3. Posterior infraorbitals expanded.
4. Caudal skeleton with two free ural vertebrae.

These four characters provide ample justification for separating the Ichthyotringidae from the Myctophiformes. Additional substantiation for the separation is provided by the time of occurrence of the two groups in the fossil record. *Apateodus* first appears in the Albian (Lower Cretaceous); *Ichthyotringa* in both the Lower Cenomanian (*Ichthyotringa africana*, Arambourg 1954) and the Middle Cenomanian (*Ichthyotringa delicata*, Hay 1903); whilst *Apateopholis*, the most specialized of the ichthyotringoids, is also from the Middle Cenomanian. Thus the Ichthyotringoidei had not only arisen but had radiated to produce highly specialized members by the beginning of the Upper Cretaceous. At an equivalent time (i.e. Middle Cenomanian) the myctophiform lineage is only represented by basal, generalized forms such as *Sardiniodes*. If the Ichthyotringoidei and the Myctophiformes are related then the myctophiforms would presumably have arisen from the ichthyotringoids. This view is clearly untenable since the Ichthyotringoidei possess several specialized characters which are more advanced than anything seen in the basal myctophiformes. These features include :

1. The long rostrum with its entailed loss of bony elements.
2. Absence of fulcral scales at the base of the tail.
3. Absence of a pelvic splint bone.
4. Absence of accessory radials in front of the dorsal fin radials.

These four factors are, however, encountered among some of the more advanced 'alepisauroid myctophiforms' (Marshall, 1955; Gosline, Marshall & Mead, 1966). For example rostral lengthening and the forward migration of the jaw articulation occur in *Lestidium* and *Anotopterus* (Text-fig. 78) and the similarity in jaw structure between *Anotopterus* and *Ichthyotringa* has been pointed out by Arambourg (1954) :

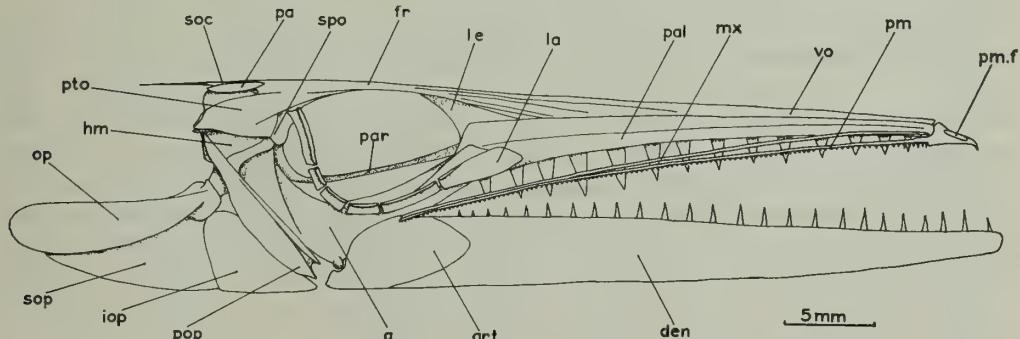


FIG. 78. *Anoptopterus pharao*. Skull in lateral view.

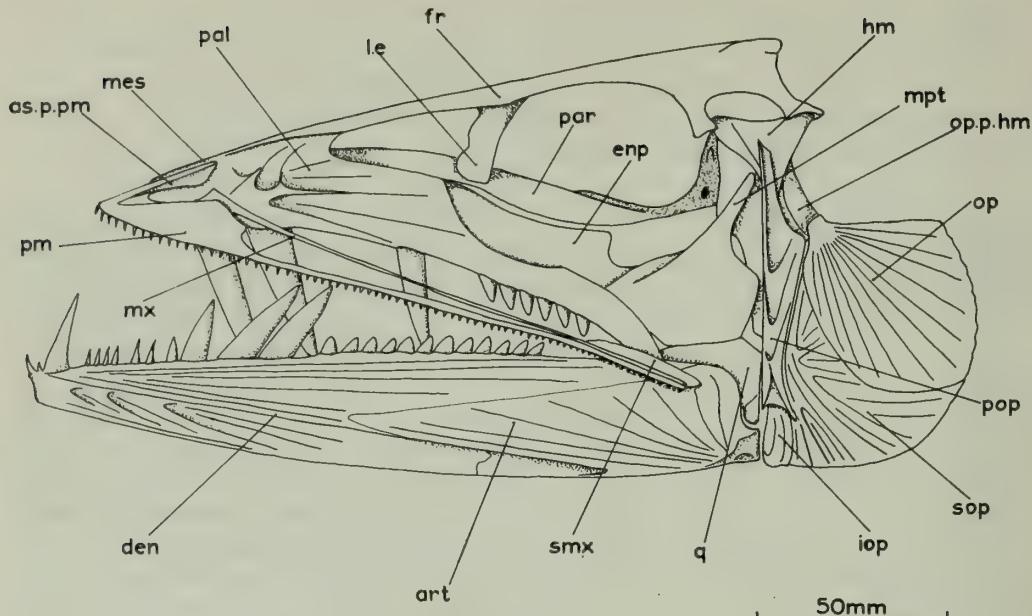


FIG. 79. *Alepisaurus ferox*. Skull in lateral view.

124). Regan (1911 : 120) has noticed the similarity between *Apateodus* (Text-fig. 11) and *Alepisaurus* (Text-fig. 79) in both of which no great rostral elongation has occurred. The composition of the snout in these two genera is also similar with an extended mesethmoid, palatine and vomer with the palatine supporting several enlarged, laterally compressed teeth. One difference is that in *Apateodus* both palatine and ectopterygoid bear teeth, whereas in *Alepisaurus* all of the teeth are borne on the palatine. The dermal upper jaws are superficially similar but *Apateodus* is more primitive in that the premaxilla does not have an ascending process, and the maxilla is a simple strut. In *Alepisaurus* the premaxilla and maxilla have been derived by simplification from a much more complex pattern. Both genera have lost the antorbital and nasals due to the elongation of the snout.

The caudal skeleton has already been mentioned as being in a condition comparable to the elopoids and salmonoids in respect of the number of separate ural vertebrae. The caudal skeleton of *Ichthyotringa furcata* (Text-fig. 4) shows a neural arch without a neural spine on the first preural vertebra which is like that seen in *Elops* (Text-fig. 80) and *Sedenhorstia* (Goody, 1969, fig. 2). In the Salmoniformes the neural arch of this vertebra is incorporated with the first uroneural (and probably the neural arch of ural vertebra one) to produce the stegural (Text-fig. 81). In *Ichthyotringa* the neural arch of preural vertebra one is distinct and the anterior uroneural is expanded anteriorly. This expansion probably represents the neural arch of ural vertebra one and thus an earlier stage in the production of a stegural, with the neural arch of preural vertebra one not having yet been incorporated. In *Elops* there is also

a small anterior expansion in advance of the first uroneural, which may well represent the neural arch of ural vertebra one. If this is the case then the forerunner of a stegural is present in the elopoids. In the Salmoniformes the epurals are associated with the dorsal edge of the stegural. In *Elops* and *Ichthyotringa* the epurals contact the dorsal edge of the anterior expansion of uroneural one. This possibly affords further evidence that the anterior expansion is the forerunner of a true stegural.

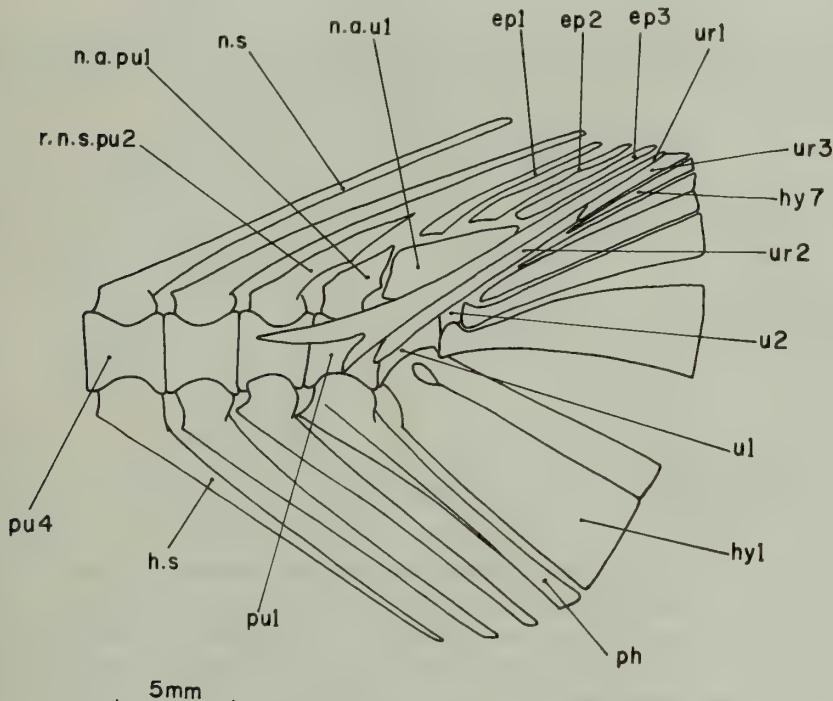


FIG. 80. *Elops saurus*. Caudal fin skeleton in lateral view.

Preural vertebra two in *Ichthyotringa* has a complete neural spine. In *Elops* this neural spine is reduced (Text-fig. 80), as it is in certain salmonoids (Norden, 1961; pl. 14, fig. G, *Coregonus artedii*). In other salmonoids the neural spine is complete (Text-fig. 81). In those forms in which a reduced neural spine occurs then three separate epurals are normally seen (the primitive teleostean number according to Patterson, 1968a : 220). *Ichthyotringa*, with its complete neural spine on preural vertebra two, has only two epurals. It would seem possible, then, that the anterior-most epural, when three are present, comes from the neural spine of preural vertebra two, the remaining two epurals being the neural spines of preural vertebra one and ural vertebra one. Patterson (1968a : 221) has drawn attention to the fact that the foremost epural can "fuse with a neural arch so that it is indistinguishable from a neural spine". It is equally possible that this is what has occurred in *Ichthyotringa*.

Ichthyotringa agrees with *Elops* but not with the salmonoids in the possession of two long, narrow, rod-like uroneurals. *Elops* has a third smaller uroneural postero-dorsally, but this is not observed in *Ichthyotringa*, although present in *Salmo* (Norden, 1961).

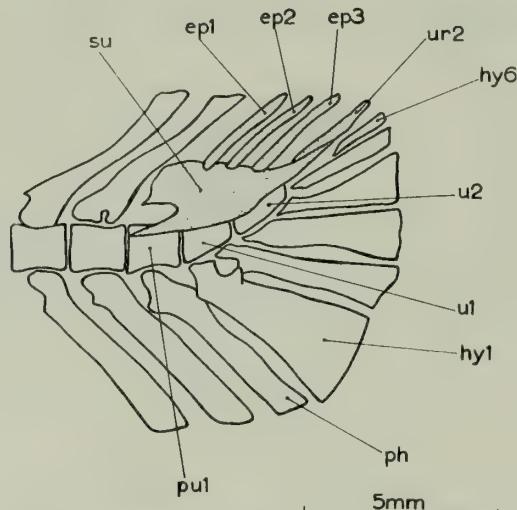


FIG. 81. *Salmo gairdneri*. Caudal fin skeleton in lateral view. After Norden (1961).

Six hypurals are evident in *Ichthyotringa* and in this respect it is comparable to the salmonoids. The elopoids have seven hypurals, the seventh very small and practically hidden beneath the third uroneural. The arrangement and size of the hypurals is of characteristic form in *Ichthyotringa*. The two ural vertebrae are much reduced in length and strongly upturned, much more so than in either *Elops* or *Salmo*. In both of these latter genera the hypurals decrease in length from hypural one to hypural six (or seven). In *Ichthyotringa* the hypurals remain quite long and there is no equivalent to Monod's (1967) "hypurale minimum", the small isolated last hypural. All of the hypurals in the upper caudal lobe of *Ichthyotringa* appear to attach to the small second ural vertebra.

All of the elopoids and the salmonoids possess 17 branched caudal rays, as does *Ichthyotringa*. In the Ichthyotringoidei and the Salmonoidei no fulcral scales occur, but these are present in the elopoids.

A feature noticed in the basal Salmoniformes is the tendency for the neural and haemal spines in the posterior caudal region to be considerably laterally compressed and expanded (Gosline, 1960; Norden, 1961; Vladykov, 1962). In the elopoids as well as in *Ichthyotringa* the posterior neural and haemal spines are long and narrow and drawn out in a posterior direction with no compression or expansion.

On tail structure the Ichthyotringoidei show marked similarities to the Elopiformes, and in other characters also resemble the elopoids, for example:

1. Roofed post-temporal fossa.
2. Orbitosphenoid and basisphenoid present.
3. Posterior infraorbitals expanded.
4. No ascending process on the premaxilla.
5. Mesocoracoid arch (*Apateodus*).
6. Abdominal pelvic fins.
7. Supraorbital bone (*Apateodus*).

These characters are all, however, merely indicative of a primitive grade of organisation, and could equally ally the Ichthyotringoidei with the salmonoids. Certain features, however, definitely separate the ichthyotringoids from the elopoids :

1. No rostral bones, and no ethmoidal commissure.
2. No antorbital.
3. No nasal.
4. No supramaxillae.
5. No gular plate.
6. Development of a trigemino-facialis chamber in the prootic (*Apateodus*) as opposed to the separate intraosseus passages seen in the elopoids (Greenwood, *et al.*, 1966).
7. No teeth on the parasphenoid.

These features are sufficient clearly to separate the ichthyotringoids from the elopoids and are features which are present in the more progressive salmoniforms. Greenwood, *et al.* (1966 : 350), in the erection of their new superorder Protacanthopterygii, suggested that the salmonoids constitute the principal and basal element of this group, possessing none of the limitations of the elopoids, and the salmonoids would appear to have the requirements to give rise to the major radiations within the Protacanthopterygii and Acanthopterygii. The salmonoids possess the following basal osteological characters : parietals in contact in the mid-line ; orbitosphenoid and basisphenoid ; supraorbital and antorbital ; expanded posterior infraorbitals ; maxilla large and toothed ; incipient ascending process of premaxilla ; two large supramaxillae ; teeth on vomer, palatine, endopterygoid and ectopterygoid ; numerous branchiostegal rays ; mesocoracoid arch ; three postcleithra ; as many as 18 pectoral rays ; anterior neural spines consisting of separate lateral elements ; numerous supraneurals ; numerous epineurals ; transverse processes not fused to centra ; pelvic fin with 11 rays ; pelvic splint bone ; no fin spines ; two free ural vertebrae ; stegural with one or two further uroneurals ; 17 branched caudal rays ; six hypurals ; cycloid scales.

The Ichthyotringoidei agree with the majority of these characters, differing in the features related to rostral elongation, and the absence of a stegural, accessory radials and a pelvic splint bone. In conclusion, then, the ichthyotringoids represent a small radiation commencing in the Lower Cretaceous. *Apateodus* is the least specialized genus and continued little changed throughout the Upper Cretaceous (Gault to Maastrichtian). It was a generalized predator which may possibly have given rise to the other more advanced ichthyotringoids. The elongate rostral region

does not appear to represent as efficient a modification for predatory feeding as does the more mobile and protrusile acanthopterygian jaw. The rise of the acanthopterygians probably accounted for the disappearance of the ichthyotringoids in the Upper Cretaceous. The more generalized *Apateodus*, however, existed until the extreme end of the Cretaceous and outlasted its more specialized descendants. The only recent teleosts which possess a long snout and an unelongated body seem to be the Xiphiidae, possibly strengthening the argument that this rostral elongation represents a less successful way of life.

The Ichthyotringoidei must have arisen as a very early offshoot from a basal salmoniform stock, a stock not too far removed from the elopiforms.

(B) Suborder CIMOLICHTHYOIDEI

This new suborder has been erected to contain several quite closely related genera, all of which are difficult to link with any Recent forms or with any so far described fossil forms. The two families Cimolichthyidae and Dercetidae show great similarities in overall skull and body structure, in particular the rostral region and the reduction of the body scaling to two or three isolated scute rows on each flank (Text-fig. 82). Both families occur in the Cenomanian and extend through much of the Upper Cretaceous. Many incomplete and fragmentary specimens of large *Dercetis* species from the English Chalk (Woodward, 1903), e.g. *Dercetis maximus* and *Dercetis laticutatus*, are closely related to *Cimolichthys levesiensis* from the same horizons. These large species of *Dercetis* have not been considered in the systematic account since they are represented by very imperfect material.

The structurally interesting features shown by the cimolichthyids and dercetids are mainly concerned with the extension of the head or body or both. These elongations of the head and body have occurred to a greater or lesser extent in all of the genera. *Cimolichthys* shows slight snout and body elongation; *Dercetis* has a variably extended snout with a long body (Text-figs. 23–26); *Rhynchodercetis* has an enormously elongated snout and a very long body (Text-figs. 28 and 29), and *Pelargorhynchus* has some snout elongation but much body lengthening.

Snout elongation is always brought about by the extension of the preorbital region and includes the vomer, mesethmoid, palatines, premaxillae, maxillae and also the frontals to a marked extent where they extend forwards between the postero-lateral arms of the mesethmoid (Text-figs. 16, 17 and 31). *Rhynchodercetis* differs very slightly from the others in that the anterior rostral region is formed solely by the premaxillae and there is a tendency for the dentary to be shorter than the rostrum (Text-fig. 29), the latter being a feature seen in several other unrelated groups, e.g. *Aspidorhynchus* and *Belonostomus* (Gardiner, 1960 : 362) among fossil halecostomes, and *Istiophorus* among Recent fish. There is obviously some correlation between the mode of life, particularly trophic habits, and the greater extension of the upper jaw, but any obvious correlation is difficult to envisage. Possibly the rostrum acted as a cutwater, reducing the amount of turbulence during forward motion and thus enabling the fish to approach its prey undetected. All the other

genera are also predatory as evidenced by the well-developed dentition on all the jaw bones. The jaw suspensorium remains vertical in position irrespective of the lengthening of the jaws and is always shallow. This factor alone tends to indicate that these genera moved on to prey slowly and undetected. A fast movement would be hazardous to the long thin jaws which would have had to have been opened during this rush.

Bodily elongation occurs within the Dercetidae as a result basically of the multiplication of vertebral elements (as many as 80 being present in *Dercetis gracilis*, Text-fig. 25). Additional lengthening is achieved by extension of the vertebral centra in the anterior precaudal region in both *Dercetis* and *Rhynchodercetis*. The outcome of this extension of the centra is a fish with a very long and narrow 'neck' region, well shown in *Dercetis rostralis* (Text-fig. 26), in which the anterior centra are as much as six times as long as they are deep. Together with the extension of the 'neck' there is the production of enlarged transverse processes projecting strongly laterally (Text-fig. 30A). Siegfried (1966 : 214) has compared the dercetids with the Gasterosteiformes in respect of the vertebral composition. Elongation of the anterior precaudal vertebrae occurs in the Aulostomoidei (*Aulostoma*) and the Syngnathoidei (*Syngnathus*), and in these genera large transverse processes occur. The gasterosteiforms are in no way related to the dercetids, since the elongate dercetid jaw is at complete variance with the very small jaws at the end of a long tubular snout encountered in the Gasterosteiformes.

In *Rhynchodercetis hakelensis* (Text-fig. 28) long, linearly arranged ossifications in the mid-dorsal line between the occiput and the origin of the dorsal fin may represent ossifications within a median dorsal ligament. If the transverse processes were in life connected one to another by ligaments, then together with the ossified dorsal ligament, the 'neck' could have been held rigidly in a straight line. Since the median fins occur in the posterior half of the body and the caudal region is relatively stout, then this may support the assumption that these fish moved slowly and stealthily towards their prey, the anterior body being held rigid and thus creating little turbulence in the water, whilst the main propulsive force is concentrated at the extreme posterior end of the body. On the other hand the modifications of the body may have enabled the fish to make a quick darting movement, this however has been shown not to be in accord with the jaw structure. Arambourg (1954 : 119) stated that *Rhynchodercetis yovanovitchi* resembled the Scomberesocidae and certain Xiphiidae, and was probably exclusively pelagic. This would seem to be a reasonable conclusion and the habit of the gar-fish, *Belone*, is closest to that of the dercetids.

Squamation in the Dercetidae is reduced to several isolated scute rows along the flanks, the major rows being composed of scales conforming to a basic triradiate plan (Text-figs. 82A-D). In general, reduction in squamation is correlated with the presence of a distensible stomach, and this is so in the dercetids, since several specimens examined contained whole fish within the body cavity (see also Woodward, 1942a : 555).

The genus *Prionolepis* has so far not been mentioned in the systematic descriptions or in the discussion. This genus, originally referred to the Enchodontidae by

Woodward (1901 : 230) presents some problems as to its relationships. It would seem to be most closely related to the dercetids and cimolichthyids as constituted in this work. Provisionally then it is placed as an addendum to the suborder Cimolichthyoidei and a new family Prionolepididae is created for its reception. There follow diagnoses and a description of the only completely preserved species, *Prionolepis cataphractus*.

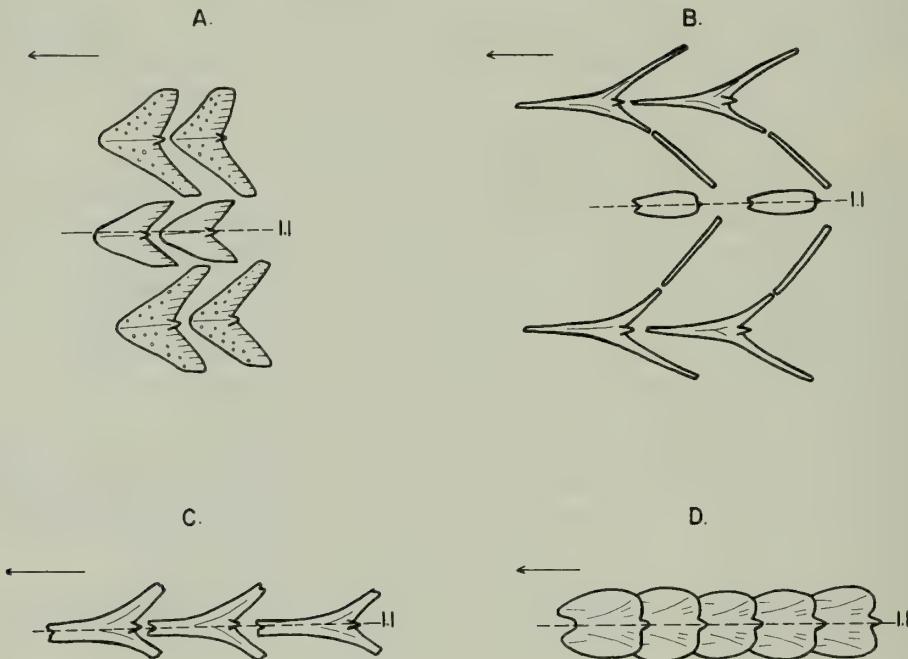


FIG. 82. Flank scutes of representative cimolichthyoids. (A) *Dercetis triqueter* Pictet. (B) *Dercetis gracilis* (Davis). (C) *Rhynchodercetis gortanii* (d'Erasmo). (D) *Pelargorhynchus dercetiformis* von der Marck.

Family PRIONOLEPIDIDAE nov.

DIAGNOSIS. Body elongated and relatively shallow, neurocranium shallow and acutely pointed anteriorly. Post-temporal fossa roofed. Mesethmoid with large ventro-laterally directed, wing-like structures. Supratemporal sensory canal on the parietals and supratemporals. Maxilla stout with two prominent rows of teeth; supramaxilla absent. Vertebrae approximately 45 in number of which at least 20 are caudal. Dorsal fin short and in the middle of the back; anal fin small and remote. Body bearing a single row of deep scutes which cover the whole flank region on either side.

Genus ***PRIONOLEPIS*** Egerton, 1850

DIAGNOSIS (emended). Prionolepididae in which the head and body are slightly elongated and somewhat laterally compressed. Teeth extremely numerous on the vomer, palatine, ectopterygoid and dentary; all teeth long, thin and needle-like and noticeably recurved. Vertebrae as long as deep with mesially constricted centra. Paired fins large, pectorals slightly larger than the pelvics. Pelvic fins opposed to the hinder part of the dorsal fin.

TYPE SPECIES. *Prionolepis angustus* Egerton.

Prionolepis cataphractus (Pictet & Humbert)
(Text-figs. 83-85)

- 1866 *Aspidopleurus cataphractus* Pictet & Humbert : 109, pl. 18, fig. 1.
1901 *Prionolepis cataphractus* (Pictet & Humbert) Woodward : 230.
Woodward lists the earlier references.

DIAGNOSIS (emended). *Prionolepis* of standard length not exceeding 19 cm. Length of head with opercular apparatus less than half the length of the body. Maximum depth of the trunk one-seventh of the body length. Dorsal fin with 18 rays; anal fin with 14 rays, nearer to caudal than to pelvics. Pelvic with 9 rays, pectoral with 13 rays. Lateral scutes 45 in number, the largest being four times as deep as broad. Hinder margin of each scute slightly pectinate, anterior margin marked with delicate and irregularly arranged vertical striations.

HOLOTYPE. Specimen number 639/59, an imperfect fish in the Museum d'Histoire Naturelle, Geneva, from the Middle Cenomanian of Hakel, Lebanon.

MATERIAL. Specimens in the B.M.N.H., numbers P.4864, P.9966, P.9967, P.9968, P.9970, P.47332, P.47516, all from the Middle Cenomanian of Hakel and Hajula, Lebanon, and all prepared by the transfer method.

DESCRIPTION. *Neurocranium*. The neurocranium is shown in dorsal view in Text-figure 83. The skull-roof is flattened and reaches its widest extent between the sphenotics at the hind end of the orbit. The frontals occupy the majority of the roof extending back almost to the occiput. The frontals contact each other in a straight suture. Laterally the frontals form the upper border of the orbits and extend on to the dorsal surface of the sphenotics. More posteriorly the frontals contact the medial edges of the pterotics in a straight suture. The frontal is ornamented with raised ridges of bone each set with minute tubercles. The ornamentation of the frontal arises from the centre of ossification above the hind end of the orbit. The ridges pass forwards towards the snout region, and also laterally above the orbit. Posteriorly directed ridges pass back on to the rear part of the frontal above the cranial cavity. Anteriorly the frontals taper most markedly from the anterior orbital region and are inserted below the posterior edge of the mesethmoid. Posteriorly the frontals overlap the anterior regions of both the parietals and the supraoccipital.

The supraoccipital contacts the frontals anteriorly, and separates the parietals. It extends down on to the posterior face of the neurocranium where it gives rise to a small backwardly directed crest which does not extend above the plane of the skull-roof. Laterally the supraoccipital meets the epiotic in a pronounced suture.

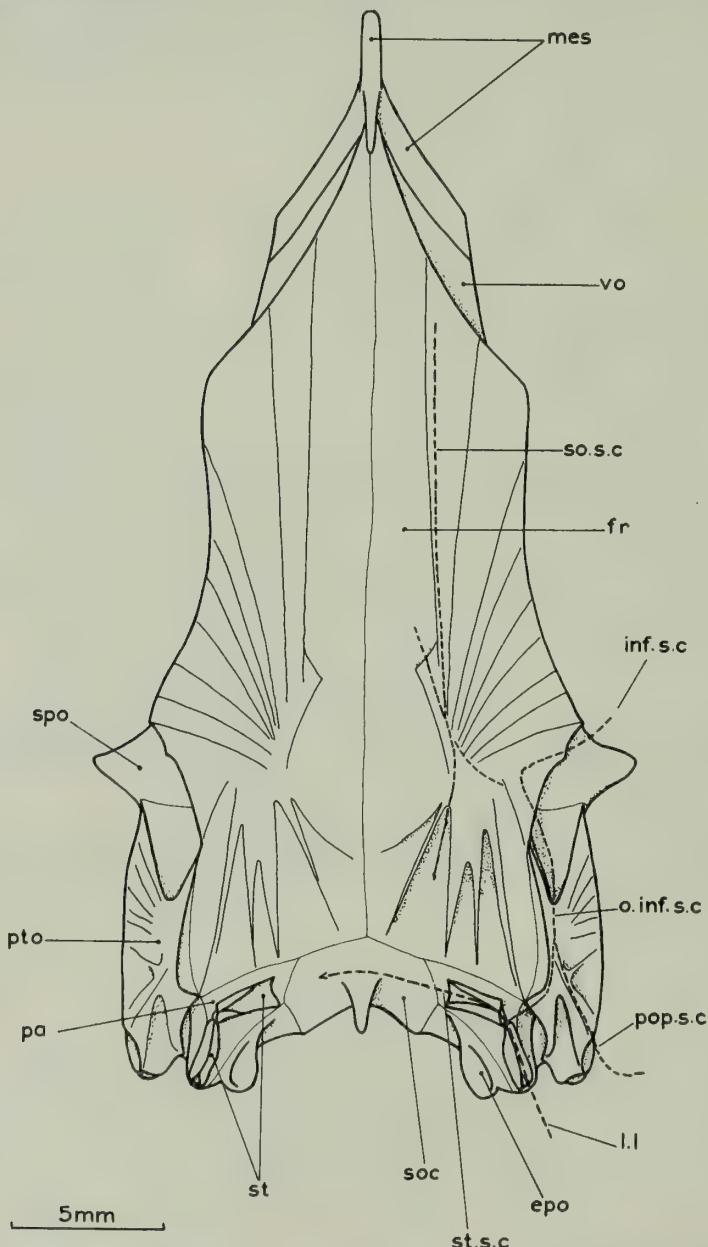


FIG. 83. *Prionolepis cataphractus* (Pictet & Humbert). Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals.

The parietals are bordered anteriorly by the frontals and posteriorly by the epiotics. The parietal is smooth apart from two small strips of ornamented bone fused to the surface. One of these strips is transversely arranged, the second longitudinally. Both the transverse and longitudinal strips contain partially roofed dorsal grooves. These two strips of bone represent the remains of a supratemporal bone, and housed the supratemporal sensory canal.

The pterotic forms the postero-lateral border of the skull-roof contacting the sphenotic anteriorly and the frontal medially. Postero-medially it is separated from the parietal and the epiotic by an indentation of the posterior edge of the skull-roof. This indentation is in the form of a narrow antero-posteriorly orientated groove, probably representing the upper region of the opening to a roofed post-temporal fossa. The dorsal surface of the pterotic is ornamented with irregular, tuberculated ridges. A tube is present within the pterotic opening anteriorly about mid-way along the bone, and posteriorly in two places. The first of these posterior openings is positioned on the edge of the pterotic and the second on the inner edge of the posterior part of the pterotic. On the lateral face of the neurocranium the pterotic makes up the major part of the hyomandibular facet. Above the hyomandibular facet the pterotic contributes towards the formation of the dilatator fossa which is an elongated oval fenestra.

The sphenotic projects laterally from beneath the frontal at the rear of the orbit. Dorsally the sphenotic joins the pterotic posteriorly, and is unornamented. Laterally the sphenotic gives rise to a stout strut passing ventro-medially to contact a corresponding strut of the prootic. Between these two struts a cup-shaped recess is produced and this forms the anterior region of the hyomandibular facet.

The course of the sensory canals is indicated both by tubes within the bone and open grooves on the surface. The supraorbital sensory canal was confined to the frontal, and opened anteriorly on the edge of the frontal in advance of the orbit : no trace of nasal bones was found in this region. Posteriorly the sensory canal passed postero-medially from the centre of ossification. The infraorbital sensory canal passed across the dorsal surface of the sphenotic and under the lateral extension of the frontal. The lateral line canal from the post-temporal appears to have divided before entering the posterior part of the neurocranium. The otic branch of the infraorbital canal entered the pterotic above the post-temporal fossa and passed forwards within the bone. Anteriorly the otic branch passed on to the dorsal surface of the sphenotic beneath the frontal to contact the main infraorbital canal. The supratemporal sensory canal is the second division of the main lateral line canal, and passed medially on to the surfaces of both of the limbs of the supratemporal. The supratemporal canal appears to have been continuous across the dorsal surface of both the parietals and the supraoccipital. The preopercular sensory canal was transmitted through a postero-lateral pore of the pterotic and joined the otic branch of the infraorbital canal within the pterotic.

The epiotics form part of the occipital border and the medial edge of the posterior part of the post-temporal fossa. The major portion of the epiotic is on the posterior face of the neurocranium. Postero-dorsally the epiotic gives rise to a smooth,

rounded, posteriorly directed flange. The dorsal surface of this flange provides the region of articulation for the dorsal limb of the post-temporal.

The mesethmoid is peculiarly shaped, appearing as two distinct portions, an anterior short, straight rod-like piece forming the extreme anterior termination of the snout; and a much expanded posterior region. This posterior region is in the form of two narrow, flattened wing-like expansions which are directed postero-laterally and inclined ventro-laterally. The lateral edge of each mesethmoid wing is attached to the dorso-medial region of each palatine.

The vomer closely parallels these lateral extensions of the mesethmoid and is attached to its ventral surface. The vomer is more extensive than the mesethmoid and gradually narrows posteriorly to contact the parasphenoid in the region of the lateral ethmoid. The palatine appears to be associated with the edge of the vomer which supports numerous teeth.

The parasphenoid is visible within the orbit where it is slightly expanded into lateral flanges which overlap the medial edges of the endopterygoids. Anteriorly the parasphenoid passes between the lateral ethmoids and attaches to the posterior end of the vomer. The lateral ethmoids meet the ventral region of the frontals delimiting the orbit anteriorly. They expand ventrally and are attached to the upper posterior end of the palatine.

Hyopalatine bones. The hyomandibular is large with an elongated head. The anterior part of this head is thickened and so shaped as to fit into the anterior cup-shaped part of the hyomandibular facet. The remainder of the head is much thinner and almost straight. The posterior edge of the hyomandibular is backwardly curved, but the posterior edge of the quadrate curves forwards so that the condyle occurs immediately below the occiput. The outer face of the hyomandibular bears one relatively prominent crest arising from the anterior region of the head and passing postero-ventrally to the hind edge of the bone.

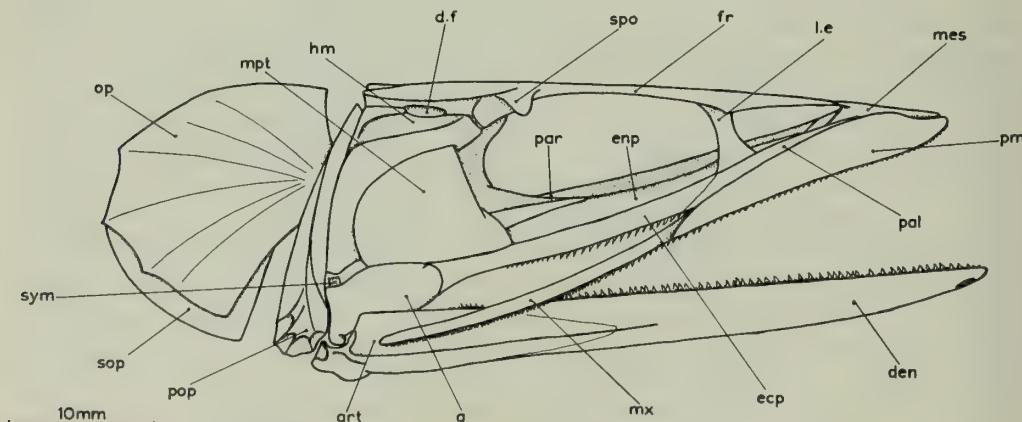


FIG. 84. *Prionolepis cataphractus* (Pictet & Humbert). Restoration of the skull in lateral view.

The quadrate is a large, triangular bone with a prominent transversely arranged condyle. The posterior edge of the quadrate is thickened and deflected laterally and bears a vertical groove posteriorly. The postero-dorsal edge of the quadrate is slightly excavated, indicating the upper limit of the symplectic groove on its medial face. The symplectic is a vertical rod-like bone, internal to the quadrate. The anterior end of the quadrate lies against the lateral surface of the posterior end of the ectopterygoid.

The ectopterygoid is a long narrow strut of bone slightly thickened posteriorly. The ventral edge of the ectopterygoid is flattened and bears teeth. Anteriorly the bone has some three rows of slender, acutely pointed recurved teeth, but more posteriorly the tooth row number decreases. The ectopterygoid contacts the palatine anteriorly and is quite firmly attached to it. The endopterygoid is plate-like and attached to the internal edge of the ectopterygoid. The metapterygoid is a very large thin sheet of bone covering most of the lateral face of the hyomandibular, contacting the quadrate and ectopterygoid ventrally and the endopterygoid anteriorly.

The palatine is elongate, stout and forms a direct continuation of the ectopterygoid anteriorly. Postero-dorsally it is attached to the ventral region of the lateral ethmoid, and anterior to this has a small dorso-laterally inclined maxillary process. The palatines are very close together at the anterior end of the snout. Ventrally the palatine is flattened and covered irregularly by teeth. The teeth are slender, acutely pointed and strongly recurved.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 84. The premaxilla is prominent, thin and elongate. Anteriorly it appears to contact its partner in the mid-line just in advance of the mesethmoid. The outer face of the premaxilla is smooth and curved. It is of relatively uniform depth along most of its length but tapers somewhat posteriorly.

The maxilla is long and slender, forming almost exactly half of the gape. The head of the maxilla is inflected and bears a medial excavation which houses the maxillary process of the palatine. The anterior region of the maxillary head is drawn out in front of this medial excavation and would appear to lie on the dorsal surface of the wing-like mesethmoid extension.

Teeth are present on both of the bones in the dermal upper jaw. The maxilla bears a double row of small acutely pointed teeth on that part of the bone which enters the oral border of the upper jaw behind the premaxilla. The teeth are inclined slightly in a posterior direction. Teeth on the premaxilla are confined to a single marginal row and are essentially similar to those on the maxilla but smaller.

Mandible. The mandible is shown in lateral view in Text-figure 84. It is long, very shallow and acutely pointed at the symphysis. The dentary forms the whole of the oral border and practically the entire ventral border and has a deeply indented posterior edge. The oral margin of the dentary supports numerous irregularly placed, small teeth. The teeth are acutely pointed and markedly recurved. Towards the posterior end of the dentary the teeth are reduced in number and confined to approximately two rows.

The articular forms the posterior region of the mandible, extending anteriorly to insert on the medial face of the dentary. Below the shallow articular facet there is a small posteriorly directed foramen which transmitted the mandibular sensory canal. This sensory canal passed within a tube of bone on the ventro-lateral edges of both the articular and dentary, and a small oval pore close to the symphysis indicates its anterior extent. The lateral face of both dentary and articular is unornamented, but the articular has a pronounced lateral flange passing forwards from in front of the articular facet. This flange decreases in size and ends near to the level of the posterior end of the premaxilla. The maxilla rests against the dorsal surface of this flange when the jaws are shut.

The angular is a small knob of bone forming the postero-ventral angle of the mandible, with its posterior face fitting against the ventral region of the preoperculum.

Opercular bones. The opercular bones are shown in lateral view in Text-figure 84. The preoperculum is deep, and narrow. Dorsally it ends posterior to the head of the hyomandibular and anteriorly lies against the posterior face of the crest on the hind edge of the hyomandibular. Ventrally the preoperculum rests in a groove on the posterior edge of the quadrate, where it is slightly expanded and bears several prominent ridges. The preopercular sensory canal ran within a tube along the length of the bone opening ventrally through three or four pores. The most prominent pore faces antero-ventrally and transmitted the main canal to the mandible. The posterior edge of the preoperculum is thin and overlaps the anterior edge of the operculum.

The operculum is large and the opercular facet occurs just within the upper half of the anterior edge. The posterior edge of the operculum is rounded dorsally, but ventrally the edge is irregularly excavated. A horizontal strengthening ridge passes across the internal face of the operculum.

The suboperculum lies ventral to the operculum and is overlain by the latter to a marked extent. The supoperculum has a smooth outline, unlike the operculum, and its lateral face is unornamented. No trace of an interoperculum was found in any of the specimens examined.

Hyoid arch. Both the ceratohyal and the epihyal are elongate, roughly rectangular ossifications, joined in life by cartilage. A prominent groove runs along the length of the lateral face of both bones and marks the course of the hyoidean artery. The hypohyals are prominent and attached to each other in the mid-ventral line. The ceratohyal is firmly attached to the posterior end of the hypohyal, and traces of a median urohyal are seen where it contacted the hypohyals. The urohyal is elongate with a shallow dorsal longitudinal crest.

Fourteen branchiostegal rays are present, the first 8 attached to the ventral region of the lateral face of the ceratohyal. These 8 rays are uniform in size and shape. The more posterior 6 branchiostegal rays articulate with the epihyal and are stouter, slightly flattened and more sharply inclined posteriorly.

Pectoral girdle and fin. The post-temporal has a flattened, oval dorsal limb articulating with the epiotic. The upper surface of the dorsal limb is ornamented with bony tubercles postero-medially. The ventral limb is in the form of a narrow antero-ventrally inclined strut. The supracleithrum articulates with a postero-medial facet on the post-temporal. The lateral line canal entered the post-temporal through a foramen in the supracleithral facet and passed through the post-temporal to emerge near its anterior end.

The supracleithrum is short and stout with an expanded, elongated, head. Dorsolaterally it is ornamented with minute bony tubercles and more ventrally with raised ridges. The lateral line canal entered the posterior region of the head of the supracleithrum and passed anteriorly within the bone.

The cleithrum is a large curved bone narrowing dorsally where it fits under the supracleithrum, and curving forwards ventrally. The anterior edge of the cleithrum is inclined medially forming the posterior boundary of the branchial opening.

The endoskeletal girdle projects behind the cleithrum, and a large scapular foramen is visible. On the posterior edge of the scapula a large saddle-shaped facet forms the articulation for the anterior fin ray. The coracoid is thinner and more membranous than the scapula and extends forwards ventrally to contact the cleithrum at its tip, thus leaving a large fenestra between the two.

Two postcleithra are present, the dorsal one being oval in shape, and attaching to the medial face of the cleithrum and supracleithrum. The ventral element is thin and curved and extends ventrally, medial to the pectoral fin.

The pectoral fin is composed of 13 rays all of which are segmented and branched distally, except for the first which is unbranched.

Pelvic girdle and fin. Each pelvic bone is an elongate triangle lying horizontally in the ventral body-wall about halfway along the length of the body, the insertion of the fin being on a level with the 21st precaudal vertebra. There is a thickened ventral flange running the length of each pelvic bone and anteriorly the bones are joined. Postero-laterally the pelvic bone is thickened to form a lateral condyle. Medial to the condyle the remainder of the fin rays articulated with an elongated facet. Medial again to this facet the pelvic bone contacts its partner in an irregular interdigitating suture. Each fin consists of 9 rays, all except the first being branched, and all segmented.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 85. It consists of 45 vertebrae of which approximately 21 are caudal. The centra are almost twice as long as deep and slightly mesially constricted. Dorsally each centrum bears a neural arch and spine, and those of the anterior precaudal vertebrae are laterally compressed and slightly expanded. The neural arches represent separate ossifications from the centra; the suture between arch and centrum is clearly visible along the entire length of the column. The precaudal vertebrae bear small transverse processes ventro-laterally on the anterior region of each centrum, with which pleural ribs articulate. The ribs are long, slender, tapering and inclined posteriorly. Each haemal arch is drawn out into a

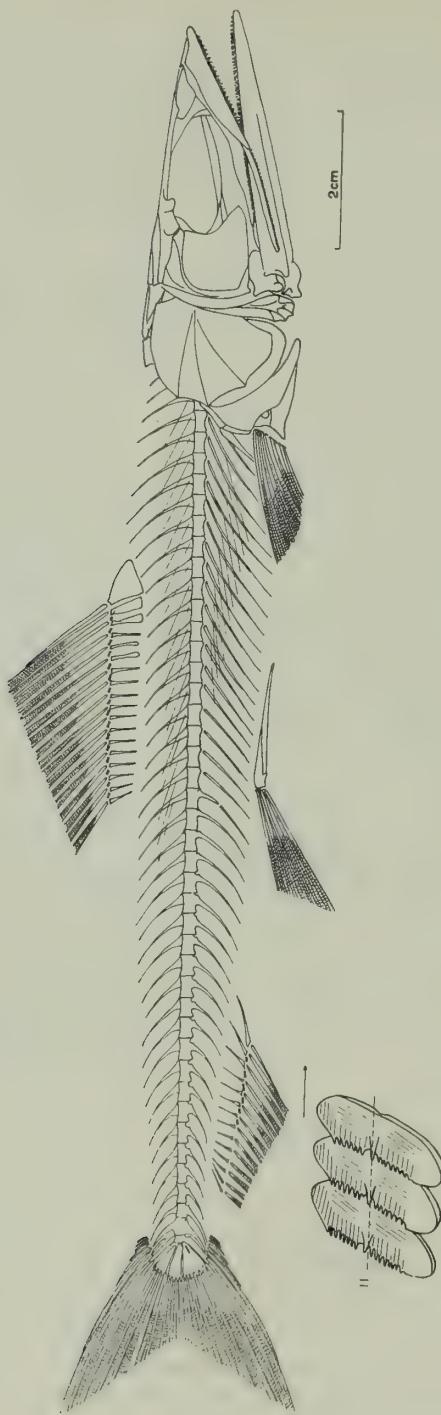


FIG. 85. *Prionolepis cataphractus* (Pictet & Humbert). Restoration of the skeleton, scales omitted. The inset shows several of the lateral line scales.

backwardly projecting haemal spine. Intermuscular bones, both epineurals and epipleurals, are present on the first 26 vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 85. The dorsal fin consists of approximately 18 rays and occurs about mid-way along the length of the body. The first ray is unbranched and shorter than the subsequent rays which are all branched and segmented. The proximal radials are elongate and the anteriormost are expanded, especially the first which bears a large forwardly directed keel-like expansion. The heads of all the proximal radials are expanded. Certain of the narrow medial radials are visible extending horizontally between the bases of adjacent fin rays.

The anal fin is made up of 14 rays and positioned at the extreme posterior end of the body close to the caudal fin. As in the dorsal fin the first ray is unbranched. The proximal radials are prominent and elongate but not expanded. Medial radials occur between the bases of adjacent fin rays.

The caudal skeleton is composed of 6 vertebrae. There are three free preural vertebrae (preurals 2, 3 and 4); one fused preural and ural vertebra (preural 1 and ural 1); and one free ural vertebra (ural 2) which is represented by a terminal half-centrum. Preurals 3 and 4 bear normal neural and haemal spines, whereas preural 2 bears an expanded haemal spine and only a neural arch, the neural spine having been lost. The compound vertebra (preural 1 + ural 1) bears the parhypural (haemal spine of preural 1) and two hypurals, the first of which is the larger. Ural vertebra 2 has approximately three hypurals associated with it making at least five hypurals in all. Associated with the dorsal regions of the ural vertebrae are two uroneural elements, which are elongated in a postero-dorsal direction. At least two epural elements are present, one of which is expanded.

Nineteen principal fin rays are present of which 17 are branched. Accessory fin rays are present above and below the fin and number at least 20.

Scales. Several of the scales are shown in the inset to Text-figure 85. They are present as a single continuous row along the lateral region of the body, and represent much enlarged lateral line scutes. The scales begin immediately behind the supracleithrum and terminate on the caudal peduncle. The row consists of 45 scutes, the most anterior and posterior ones being the smallest. Most of the scutes are about three times as deep as they are broad and the lateral line canal ran within their centres. The scales overlap and posteriorly are irregularly serrated. In the region of the lateral line there is a somewhat deeper indentation of the rear margin which is overhung by a backwardly projecting spine. The anterior edge of each scale is thickened and dorsally and ventrally the edges are rounded. The scales are obliquely inclined and ornamented with ridges on their exposed portions. The posterior part of the lateral face bears horizontally arranged ridges, whilst the anterior regions have vertically arranged ridges. Towards the caudal peduncle the scales become reduced in depth but the backwardly projecting spines become more prominent so that pronounced lateral flanges are produced on either side of the tail.

From the above description it can be seen that *Prionolepis* does share certain common characteristics with the Cimolichthyoidei. The skull roof is similar, with

the roofed post-temporal fossa ; the small, discrete laterally facing dilatator fossa above the hyomandibular facet ; toothed vomer ; simple nature of the premaxilla ; long narrow maxilla which rests on a shelf on the lateral face of the mandible when the mouth is closed ; vertical jaw suspension ; absence of an interoperculum ; presence of numerous intermuscular bones, and abdominal pelvic fins.

The rostral region of *Prionolepis* is somewhat lengthened, much as in *Cimolichthys*, but the body is little elongated. One of the most distinctive features of *Prionolepis* is the mesethmoid arrangement (Text-fig. 83). The anterior rod-like portion with which the premaxillae associate and the two large postero-laterally arranged flattened wings are different to the condition of this region in either *Cimolichthys levesiensis* or the dercetids. However in *Cimolichthys nepaeolica* from the Niobrara Chalk of Kansas, the mesethmoid arrangement approaches the condition in *Prionolepis*. As with *Cimolichthys levesiensis* (p. 40, Text-fig. 16), *Cimolichthys nepaeolica* (Hay, 1903, fig. 69) has the same large backwardly divergent laminae, but anteriorly there is a forwardly projecting prominence closely resembling the straight rod-like piece in *Prionolepis cataphractus* (p. 182, Text-fig. 83). This mesethmoid arrangement appears to be distinct from all other teleost groups and provides good evidence for the relationship between *Cimolichthys* and *Prionolepis*.

There are no expanded transverse processes on the precaudal centra, in this respect differing markedly from the Dercetidae. *Cimolichthys*, however, also has no such expanded processes although it is obviously closely related to the dercetids. The deepened, shield-like flank scutes in *Prionolepis* are of interest (Text-fig. 85) since they show signs of being feebly ctenoid. However the scales look more like the pectinate scales of *Lepidotes* rather than true ctenoid scales. The deepened flank scutes recall those of *Aspidorhynchus* and *Belonostomus* (Gardiner, 1960), and among recent fish similar scutes are exhibited in the Gasterosteiformes. It is of interest to note that in the gasterosteoids the flank scutes are supported on large transverse processes.

The systematic position of the Cimolichthyoidei is not at all clear. Pictet (1850) originally used the family Dercetidae (Hoplopleuridae) to include the genera *Dercetis*, *Leptotrachelus*, *Pelargorhynchus*, *Saurorhamphus* and *Eurypholis*, being those fishes devoid of normal squamation but possessing isolated scute rows. Woodward (1901 : 171) used Pictet's family Dercetidae but removed *Saurorhamphus* and *Eurypholis* to the Enchodontidae. Since 1901 one further genus has been added by Arambourg (1944 : 281), *Rhynchodercetis*.

The dercetids in the past have been associated with one or another of two major groups. Woodward (1901) related the dercetids to the halosaurs and notacanths. Jordan (1923 : 128) more or less concurred and grouped the Dercetidae (now including *Prionolepis* and *Leptecodon*) in the order Heteromi stating that they were close to the notacanthids.

The more predominant line of thought, however, has been that the dercetids are more nearly related to the myctophiform assemblage. Regan (1911 : 120) stated that the orbital, postorbital and post-temporal parts of the Dercetidae resembled *Evermannella*, whilst the ethmoid region and jaws resembled *Alepisaurus*.

Gregory (1933 : 201) placed the dercetids in the Heteromi but stated that any similarities with the notacanths must be put down to convergence. Authors since that time (Berg, 1940 ; Bertin & Arambourg, 1958 ; Romer, 1966) have retained the Dercetidae within the Myctophiformes following Regan's (1911) tentative proposals.

The association of the dercetids with the notacanths is obviously incorrect due to several basic dissimilarities, for example the complete regression of the caudal fin skeleton, the small inferior mouth and the snubbed rostrum of the notacanths are vastly different to those of the dercetids. Greenwood *et al.* (1966) have placed the notacanths in the Elopomorpha, and following Arambourg (1954) placed the Dercetidae in the myctophiforms.

The Cimolichthyoidei would appear not to be related to the myctophiforms because of certain primitive features which are not seen in the basal myctophiform stock, for instance, the absence of an ascending process and the toothed maxilla with no supramaxillae.

The Cimolichthyoidei as a group were relatively numerous, especially the smaller dercetids, and extended throughout the Upper Cretaceous (except for the Maastrichtian). The first genus to appear in the fossil record is the advanced *Rhyncho-dercetis*, in the Lower Cenomanian. The less advanced genera *Cimolichthys* and *Dercetis* do not appear in the record until the Upper Cenomanian. Thus the small cimolichthyoid radiation must have originated within the Lower Cretaceous. The advanced characteristics shown by the group exclude them from having given rise to any other salmoniform. These advanced characteristics are as follows :

1. Parietals separated in the mid-line.
2. Orbitosphenoid, basisphenoid and antorbital absent.
3. Interoperculum absent.
4. Reduced squamation.
5. Abnormal transverse processes and lengthened centra.
6. Overall snout and body elongation.

Several of these advanced features also preclude the cimolichthyoids from having given rise to the Myctophiformes. The Cimolichthyoidei also retain many primitive characters in common with other members of the Salmoniformes such as :

1. Partially or completely roofed post-temporal fossa.
2. Maxilla enters the gape and is toothed.
3. No ascending process on the premaxilla.
4. Supratemporal present.
5. Teeth on vomer and endopterygoid.
6. Supraorbital present.
7. Complex trigemino-facialis chamber.
8. Abdominal pelvic fins.
9. Epineurals in abundance.

Despite the fact that the cimolichthyoids are in no way related to the myctophiforms the two groups show a considerable degree of parallel evolution. For example

the caudal skeleton in the Cimolichthyoidei, as represented by *Prionolepis*, is practically identical to that of the Cretaceous myctophiform *Sardiniooides* (Text-fig. 72) and the Recent *Aulopus* (Text-fig. 93). In both the Cimolichthyoidei and the basal myctophiforms the first preural vertebra is fused with the first ural vertebra ; ural vertebra two is present as a small half-centrum supporting hypurals 3, 4, 5 and 6 ; a stegural is formed from uroneural one and the neural arches of ural vertebra one and preural vertebra one ; the neural spine of preural vertebra two is reduced so that only an expanded neural arch occurs. However a primitive feature of the myctophiform tail is the presence of basal fulcral scales both above and below the peduncle, these are absent in the cimolichthyoids. Apart from the tail other comparative points can be made between the cimolichthyoids and the more advanced 'alepisauroid' myctophiforms. For instance the parietals are separated by the small supraoccipital in both groups. Nasal bones are absent in the cimolichthyoids, either having been lost, or more likely incorporated into the mesethmoid as a result of the lengthening of the rostrum. This fusion of the nasal with the mesethmoid also occurs in several advanced myctophiforms, e.g. *Lestidium*, *Anotopterus*, *Alepisaurus* (Parr, 1929 : 28, 34). Further the cimolichthyoïd jaw resembles that seen in the 'alepisauroid' myctophiforms, except for the exclusion of the maxilla from the gape in the latter. In the cimolichthyoids (Text-fig. 21) the premaxilla does extend back for a considerable length below the maxilla, but never has an ascending or an articular process. The maxilla is reduced to a narrow strut of bone entering the gape posteriorly, and never has articulatory head processes. In *Alepisaurus* (Text-fig. 79) on the other hand, the upper jaw, although at first sight simple and similar to that of the cimolichthyoids, has been derived from a much more complex condition. In the earlier myctophiforms the premaxilla possessed an articular and an ascending process, while the maxilla had a differentiated head and supported two supramaxillæ. As a result of specialization the articular process and the supramaxillæ have been lost and the maxillary head is simplified. As in the cimolichthyoids this specialization is concerned with the lengthening of the rostral region. Other than this the cimolichthyoids still bear teeth on the vomer and the endopterygoids whereas in the advanced 'alepisauroids' these teeth have been lost.

In the cimolichthyoids barbed teeth occur on the palate and the ectopterygoid (Text-fig. 20) and serve to increase the total cutting edge of the teeth. Similar teeth are seen on the glossohyal (tongue) of *Scopelarchus*, but not elsewhere in any other myctophiform (Parr, 1929).

No traces of an interoperculum have been found in the cimolichthyoids. This feature is difficult to account for but might in some measure be due to the retention of an upright suspensorium, since the interoperculum is often small in forms with a vertical preoperculum. In *Alepisaurus* (Text-fig. 79) and *Omosudis* the suspensorium is upright and the interoperculum minute, possibly indicating a stage in the disappearance of this bone.

The transverse processes in the dercetids project strongly in a lateral direction, while *Synodus* among the recent myctophiforms has transverse processes which project ventrally. Two pairs of transverse processes are present on each centrum in

Synodus, as in *Rhynchodercetis* (Text-fig. 30A). What particular function they serve in *Synodus* is difficult to imagine. Rosen (1964 : 255) has pointed out the presence of many long, rod-like ossifications in the mid-dorsal line of *Synodus* anterior to the dorsal fin. Thus an analogous situation is found to that in *Rhynchodercetis*, in that these ossifications in *Synodus* may help to keep the body rigid. *Synodus* is a benthonic form which rests on the bottom waiting for its prey. Probably the anterior region of the body is held rigid while it makes a quick darting movement towards its prey. Gosline, Marshall and Mead (1966 : 7) indicate that *Synodus* is capable of burying itself in sand, and the rigidity may be of use here.

Reduction of the squamation is common among the most advanced myctophiforms which possess a distensible stomach. There is no equivalent reduction to the several isolated scale rows seen in the Cimolichthyoidei ; lateral line scales may remain, however, on otherwise naked forms.

The few points discussed above have illustrated that the cimolichthyoidei are neither halosaurs nor myctophiforms, although similarities are shown. The Cimolichthyoidei most conveniently fit into the order Salmoniformes (*sensu* Greenwood, *et. al.*, 1966), and represent a minor radiation which has evolved along similar lines to those within the Myctophiformes. Like the Myctophiformes the Cimolichthyoidei belong within the superorder Protacanthopterygii (*sensu* Greenwood, *et. al.*, 1966).

In conclusion the possession of a long snout and a long body would not seem to be the ideal prerequisites for a highly successful predator. Extant predatory forms possessing these characters are few in number, in fact the Belonidae would seem to be the only group (Bertin & Arambourg, 1958). Thus, in Recent fish, there seems to be little scope for a specialization of this kind to occur, since it would not result in as efficient or versatile a predatory form as a less specialized acanthopterygian. This factor might in part account for the disappearance of the Cimolichthyoidei once the radiation of the beryciforms and perciforms got under way at the end of the Cretaceous.

(C) Suborder ENCHODONTOIDEI

The first attempt to collect the enchodonts into a distinct group was made by Woodward (1901 : 189) when he erected the family Enchodontidae within the Isospondyli. This family he divided into two main sections dependent on whether a single terminal palatine tooth was present or not. In the first section (those with an enlarged terminal tooth) he included *Enchodus*, *Palaeolycus*, *Eurypholis* and *Saurorhamphus*. In the second section he included *Halec*, *Cimolichthys*, *Prionolepis*, *Leptecodon* and *Pantopholis*. Since 1901 three further genera have been included within the family, these are *Apateodus* (Woodward, 1903), *Volcichthys* (d'Erasmo, 1946) and *Rhabichthys* (Arambourg, 1954).

The suborder Enchodontidae as presented in this work only includes those genera which Woodward (1901) separated as possessing an enlarged palatine tooth. These four genera have been distributed between two families, the Enchodontidae containing *Enchodus* and *Palaeolycus*, and the new family Eurypholidae containing *Eurypholis* and *Saurorhamphus*.

The first obvious difference between the two families is the structure of the neurocranium and in particular the skull-roof (compare Text-figs. 32 and 44). In the Enchodontidae the roof inclines ventrally in its postero-lateral region due to the disappearance of the roofs of both the post-temporal and dilatator fossae. In most forms in which the roof of the post-temporal fossa is lost the reduction is correlated with the tendency for the body to become deepened post-cranially. The epaxial musculature of the 'neck' region in deeper bodied fish passes antero-ventrally to insert on to the rear end of the skull, the skull-roof and into an unroofed post-temporal fossa. In shallow bodied fish the epaxial musculature passes directly anteriorly and attaches solely to the rear face of the neurocranium or into a roofed post-temporal fossa. This latter condition is seen in the second family, the Eurypholidae (Text-fig. 47), where the body is undeepened, the skull-roof flattened and the post-temporal fossa roofed. In the Enchodontidae the loss of the roof of the post-temporal fossa is associated with a general trend towards body deepening (Text-fig. 41). Probably correlated with this postcranial deepening is the tendency for the body to become laterally compressed. Throughout the Enchodontidae the body is stouter in relation to the head than it is in the Eurypholidae. *Eurypholis boissieri* (Text-fig. 47) has an enormous head compared to the body, and far from exhibiting any postcranial deepening the body appears slightly dorso-ventrally flattened. The overall neurocranial depth is greater in *Enchodus* than in *Eurypholis*, and the hyomandibular is deeper. Both of these factors are again correlated with the overall tendency for the deepening of the body in the Enchodontidae as opposed to the Eurypholidae.

Body elongation has occurred in both of the families. In the Enchodontidae, *Palaeolycus* has a typical enchodontid head region (comparable to the genus *Enchodus*) but the body has become greatly extended by the multiplication of the vertebrae, so that upwards of 70 are present (Text-fig. 43). A corresponding elongation has occurred in the anal fin. Within the Eurypholidae, *Saurorhamphus* has an elongated body together with an elongated snout (Text-fig. 55). The body is, however, extended not by the multiplication of vertebrae but by the lengthening of the precaudal centra.

The paired fins and associated fin girdles differ somewhat in the two families. The Enchodontidae possess a 'normal' pectoral girdle with a relatively unexpanded, curved cleithrum and the pectoral fin is low on the flank (Text-fig. 40). The pelvics are abdominal, lying below the origin of the dorsal fin, with a tendency to be reduced in size somewhat. *Palaeolycus* has a minute pair of pelvics but the pectorals are enlarged. In contrast, the Eurypholidae have rather more specialized paired fins. The cleithrum is greatly expanded both anteriorly and posteriorly, and ventrally is turned in towards the mid-line (Text-fig. 46). The cleithrum is extensively ornamented and posteriorly extends below the fin insertion. The pectoral fin is much higher on the flank than it is in the Enchodontidae. The pelvic bones are large and stout and positioned directly behind the posterior cleithral extension. The pelvic fins themselves are thus in a sub-thoracic position and are larger than the pectorals.

Both families have a reduced squamation, scales being present only along the lateral line and in the mid-dorsal line anterior to the dorsal fin. In the Enchodontidae this squamation is further reduced and neither the mid-dorsal scutes nor the lateral line scales overlap. The mid-dorsal scutes are most prominent in the undepened species, e.g. *Palaeolycus dreginensis* (Text-fig. 43), and are smallest in those species of *Enchodus* which have some post-cranial deepening, e.g. *Enchodus marchisetii* (Text-fig. 41). In the Eurypholidae both series of scutes are well developed, especially those in the mid-dorsal line. In *Eurypholis boissieri* there is evidence that a sensory canal passed through the mid-dorsal scutes (p. 110). This median sensory canal presumably connected with the supratemporal commissure on the supraoccipital (Text-figs. 44 and 49). The lateral line scales are larger and more prominent in the Eurypholidae, but in both families the scales are of identical shape. Each scale bears a small pointed prominence. The prominence is smallest at the anterior end of the lateral line, but towards the caudal peduncle the spines become produced into larger hook-shaped projections. This increase in size is most marked in the Enchodontidae (*Enchodus major*) where the last lateral line scale bears a large, pointed horizontal flange projecting outwards and backwards. Monod (1959) noticed a similar latero-caudal spine in *Acanthurus monroviae* formed from a modified scale. Monod found no intrinsic musculature in the spine and it did not secrete venom, but he could give no suggestions as to its function. It can only be suggested that the spine in *Enchodus* may have had some stabilizing effect during swimming, or possibly an offensive effect if the tail was thrashed through the water.

These familial differences can possibly be related to a basic divergence in habitat and mode of life. Both families are clearly composed of predatory species with streamlined bodies, stout jaws, and a formidable armament of teeth. The Enchodontidae, with their slightly deepened, laterally compressed bodies, appear to have been active mid-water or pelagic predators. The Eurypholidae, on the other hand, with their lean, shallow, slightly dorso-ventrally compressed bodies, were probably bottom dwellers. The great expansion of the cleithra ventrally in the Eurypholidae possibly offered a protection against abrasion. In *Eurypholis boissieri* and *Saurorhamphus freyeri* the ventral edge of the mandible is strongly inclined medially and the mandibular sensory canal is enclosed within a tube for most of its length. In the Enchodontidae no such medial inclination of the mandible occurs and the sensory canal is housed in a shallow groove. Thus in the Eurypholidae both throat and sensory canal are protected from abrasion. The pelvic fins in the Eurypholidae are sub-thoracic and enlarged and possibly these may have served as supports on which the fish rested on the bottom. This last fact, that of waiting for the prey, is in part substantiated by the leanness of the body indicating some muscular reduction. Additional components of the sensory canal system on the dorsal surface of the Eurypholidae probably increased the perceptiveness to stimulation from above. Gosline, Marshall and Mead (1966 : 7) have considered a similar aspect in relation to the frontal commissure of the supraorbital canals in the Myctophiformes. In no other teleosts, living or fossil, can I find a mid-dorsal sensory canal like that of the Eurypholidae.

Despite these different modes of life the two families share a common jaw structure and mode of functioning. This aspect together with a discussion on the status of the ascending process of the premaxilla has been considered by the author in a separate paper (Goody, 1968).

The relationships and affinities of the enchodontoids have not, hitherto, been more than scantly covered. Woodward (1901 : 189) placed the family within the Isospondyli close to the Scopelidae, indicating that their nearest living relatives were the Omosudidae and the Alepisauridae. In the introduction to volume 4 of his " Catalogue " (1901), Woodward stated that, " The Enchodontidae represent a very abundant family which might furnish the ancestors of both the Isospondylous Scopelidae or the Acanthopterygian Berycidae ". Regan (1911 : 120) put the family in the Iniomi within the Isospondyli, corresponding roughly to Woodward's (1901) designation, but related them closer to the stomiatoids. Jordan (1923 : 126) followed Regan in relating them to the stomiatoids. Gregory (1933 : 204) placed the family within the group Mesichthyes (intermediate teleosts), and pointed out the divergence of opinion between Woodward (1901) and Regan (1911) as to their affinities, either scopeloid or stomiatoid respectively. Berg (1940 : 432) erected the new suborder Enchondontoidei within the Clupeiformes to contain the single family Enchodontidae, related to the stomiatoids. Bertin and Arambourg (1958 : 2268), realigned the family with the myctophiform fishes, putting them within the suborder Alepisauroidei.

Previous opinion then, has been to associate the enchodontoids with either the stomiatoids or the myctophiforms, although general agreement has been reached in assuming the enchodontoids to be relatively primitive and close to the base of the teleost radiation.

The stomiatoids are a pelagic or bathypelagic group of fishes of uncertain affinities. Beebe and Crane (1939) indicated that they were more closely related to the salmoniform fishes than to the clupeoids. This view has now been amply justified by Weitzman (1967), who has derived the stomiatoids from a stock close to the osmerids. Several features shown by the stomiatoids tend to nullify any proposition that the enchodontoids are either ancestral or even related to the stomiatoids. Certain of these are as follows :

1. In jaw structure there is a certain degree of similarity between the enchodontoids and stomiatoids in that both possess a very strongly developed dentition. In the stomiatoids, however, the major tooth bearing bones are the premaxilla and maxilla, while the palato-pterygoid dentition is reduced or absent (Weitzman, 1967 : 516, fig. 8). In the enchodontoids the palato-pterygoid dentition is strongly developed but that on the premaxilla and maxilla is reduced.
2. The maxilla of the stomiatoids is the major component of the dermal upper jaw and supports supramaxillae (Weitzman, 1967 : 516, fig. 9). In enchodontoids the premaxilla is the major bone and the maxilla is variously reduced and never bears supramaxillae.
3. There is considerable bone reduction in the stomiatoids, particularly in the neurocranium where the lateral prootic walls are lost in the anterior region of the

myodome (Greenwood, *et al.*, 1966 : 372, fig. 5), but a large basisphenoid is retained. In enchodontoids the basisphenoid is never present and the prootic is complete.

4. The shape of the ethmoid region in stomiatoids (Weitzman, 1967 : 514, fig. 7) is also quite unlike that of the enchodontoids.

5. The peculiar specialization of the anterior vertebrae of the stomiatoids (Regan & Trewavas, 1930) also sets them apart from the enchodontoids.

These five points provide sufficient evidence to assume that the two groups are not closely related. They do, however, share the features that ally them to the salmoniform complex within the Protacanthopterygii, for example, no fin-spines, abdominal pelvics, large number of branchiostegal rays, etc. A further feature which is shown by both groups is an adipose fin. This structure, or rather an impression of it in the matrix, is seen in a specimen of *Enchodus gracilis* from Sendenhorst, Westphalia (Woodward, 1901 : 202). Impressions of an adipose fin are also seen in other specimens from Sendenhorst e.g. *Sardinioides monasteri*.

The second major group with which the enchodontoids have been linked is the scopelids (Myctophiformes), and Woodward (1901) went as far as to suggest that they might furnish the ancestors of the myctophiforms. The hypothesis is untenable in the light of the host of specialized features in the enchodontoids which are more advanced than those shown by the basal myctophiform stock (e.g. *Sardinioides* and *Aulopus*). These specialized enchodontoid features are as follows :

1. Basisphenoid and orbitosphenoid absent.
2. Supraorbital and antorbital absent.
3. Nasal bones absent.
4. Supramaxillae absent.
5. Interoperculum absent.
6. No fulcral scales at the base of the tail.
7. Incomplete squamation.
8. No pelvic splint bone.

These features which are absent or reduced in the enchodontoids are present in *Aulopus*, and all except the supraorbital are present in *Sardinioides*. Thus although the enchodontoids could not conceivably be ancestral to the Myctophiformes, they could still possibly be related to them. Again this latter proposition is negated by several factors :

1. The maxilla enters the gape and is toothed in some genera of enchodontoids. In the Myctophiformes the maxilla never enters the gape and is never toothed.

2. The premaxillary region in the enchodontoids might also set them apart since all of the Myctophiformes possess a true ascending process and an articular process. The enchodontoids do not appear to have a true ascending process, but have an enormously expanded articular process (Goody, 1968 : 228).

3. The occurrence of the two groups in the fossil record also clearly separates them. At the base of the Cenomanian the Myctophiformes is represented by the primitive and generalized *Sardinioides*. The enchodontoids first occur in the Lower Cenomanian (*Enchodus venator* Arambourg, 1954 : 125) and are considerably more advanced in structure than the basal myctophiforms.

Presumably because of their similar habits, similar derivation from a salmoniform stock and similarity in evolutionary potential, many parallels can be drawn between the enchodontoids and the more advanced 'alepisauroid' myctophiforms (Marshall, 1955).

The first, and most striking, similarity between the enchodontoids and the advanced myctophiforms is the size and profusion of the buccal teeth. In both groups the dentition is concentrated on the palato-pterygoid, being absent from the vomer and only *Enchodus* showing a few scattered teeth on the endopterygoids. The structure of the palate, however, is somewhat different in the two groups. The palatine of the 'alepisauroids' is extended and bears a row of large teeth, whereas the ectopterygoid remains short and often has no teeth (Text-figs. 78 and 79). In the enchodontoids the palatine always bears a single terminal tooth and the ectopterygoid is more extensive and supports a row of large teeth. The end product is the same in that the palato-pterygoid is straight and bears a row of large ventral teeth.

Great similarities are apparent in the structure of the dermal upper jaw, excluding whether the maxilla enters the gape or not. The fenestrated premaxillary pedicel in the enchodontoids is considered by Goody (1968 : 228) to be an enlarged articular process. A similar complex is seen in *Lestidium* and *Anopterus* (Text-fig. 78) which both possess a true fenestrated ascending process, through which the slightly enlarged anterior dentary tooth projects much as in the enchodontoids. In *Omosudis* and *Alepisaurus* (Text-fig. 79) the premaxilla has a deep groove, rather than a discrete fenestra, between the narrow, attenuated ascending process and the expanded articular process. The maxillary head in the enchodontoids and the 'alepisauroids' is similar in being simple. However that of the enchodontoids would appear to be primitive, whereas that of *Alepisaurus* is derived by simplification from a more complex pattern seen in the basal myctophiform stock.

Some of the smaller skull bones which are present in the basal myctophiform stock are lost in the more advanced members and in this respect the advanced myctophiforms resemble the enchodontoids more closely. For example, the nasals become fused with the modified mesethmoid in 'alepisauroids' and in the enchodontoids the nasals are presumed to have disappeared completely. Supraorbitals and antorbitals are also absent in both groups. The basisphenoid and orbitosphenoid, which are both absent in the enchodontoids, are represented through all stages of reduction including total loss in the 'alepisauroids' (Parr, 1929). Excluding the mesethmoid region, the neurocranial structure of *Enchodus* and *Alepisaurus* is somewhat similar as Goody (1968 : 229) has shown.

In the Enchondontoidei an interoperculum is absent; this peculiarity has also been observed in the suborder Cimolichthyoidei (p. 190). Several of the more advanced myctophiforms (*Omosudis*, *Alepisaurus*, *Evermannella* and *Scopelarchus*) have a much reduced interoperculum which is possibly in the process of being lost. It would appear that forms retaining a vertical suspensorium tend to have reduced interopercula, since presumably it no longer has a functional significance.

Within the Enchondontidae (*Palaeolycus*, Text-fig. 43) there is a tendency for the body to become lengthened. This tendency is exhibited in the advanced 'alepi-

sauroids'. In both groups however the pelvics remain abdominal in position, and Marshall (1961 : 367) has indicated that the position of the pelvics in the myctophiforms is correlated with the mode of life, rather than being correlated with locomotion as in the Acanthopterygii, the bathypelagic myctophiforms having in general abdominal pelvics, whilst the benthonic groups have sub-thoracic pelvics. This assumption substantiates one aspect concerned with the division of the enchodontoids into pelagic and benthonic families since the Enchodontidae with abdominal pelvics were probably pelagic whilst the Eurypholidae with sub-thoracic pelvics were benthonic.

The caudal skeleton is very similar to that of the cimolichthyoids. The tails of *Enchodus* (Text-fig. 42) and *Eurypholis* (Text-fig. 48) are remarkably alike and show features which duplicate those seen in *Sardiniooides* (Text-fig. 72) and *Aulopus* (Text-fig. 93) among the Myctophiformes, and *Prionolepis* in the Cimolichthyoidei. These features include :

1. The fusion of preural vertebra one with ural vertebra one, the compound centrum so produced supporting a stegural.
2. The second ural vertebra present as a terminal half-centrum supporting four upper hypurals.
3. Preural vertebra two has no neural spine, simply an expanded neural arch.

The absence of basal fulcral scales above and below the caudal peduncle in the enchodontoids is as in *Prionolepis*. Both *Sardiniooides* and *Aulopus* possess fulcral scales and are thus on a more primitive level in respect of caudal structure than the enchodontoids.

The squamation of the Enchontotoidei is greatly reduced as it is in the 'alepisauroids'. This reduction is no doubt correlated with a distensible stomach (as in the Cimolichthyoidei, p. 191).

In conclusion then, the suborder Enchontotoidei has two families of divergent habitat. The order Myctophiformes, likewise, is frequently divided into two main groups, and as Gosline, Marshall and Mead (1966 : 6) have pointed out the anatomical differences between the two groups may reflect differences in environment as much as in ancestry. These authors tentatively suggest that the Myctophiformes was originally a benthonic group and cite the presence of a sensory canal commissure across the frontals as evidence. In *Eurypholis* a median dorsal sensory canal is present behind the occiput and probably served the same function. The only other character which the Eurypholidae possess which is not present in the Enchodontidae is a roof to the post-temporal fossa. This fact would tend to indicate that the Eurypholidae is the more primitive of the two, but in most other respects the Eurypholidae show specializations suiting them to a benthonic existence. Thus the Enchontotoidei are best looked on as being derived probably from a pelagic ancestral stock within the Salmoniformes which evolved to produce a benthonic group as well as retaining its original pelagic habit.

(D) Suborder HALECOIDEI

Three quite closely related genera, *Halec*, *Phylactocephalus* and *Hemisaurida* are included in this new suborder. There is a closer affinity between *Halec* and *Phylactocephalus* than between either of these and *Hemisaurida*.

Halec has a relatively shallow head and body with certain advanced characteristics, particularly in respect of the neurocranium. These features are :

1. Unroofed post-temporal fossa.
2. Parietals separated in the mid-line.
3. No basisphenoid.
4. No orbitosphenoid.
5. No supratemporal.
6. Simplified trigemino-facialis chamber.

All of these features are normally associated with advances encountered in the acanthopterygian grade (Patterson, 1964). The more primitive features seen in the genus are concerned with the body and are as follows :

1. Pectoral girdle with mesocoracoid arch.
2. Abdominal pelvic fins.
3. Incompletely fused vertebral elements.
4. Numerous intermuscular bones.

The genus *Phylactocephalus* agrees with *Halec* in respect of the skull structure, but exhibits several more advanced features associated with the body. For example, the body is shortened (33 vertebrae, whereas *Halec* has 40 to 45), and the depth of both head and body are considerably greater than in *Halec*. Correlated with body shortening is the relative position of the fins, the dorsal having advanced and the pelvics having migrated to practically a sub-thoracic position. This migration may, however, merely be a further expression of the overall body shortening, rather than a major morphological, and presumably functional migration, since the pectorals still remain low down on the body. Also the pectoral girdle of *Phylactocephalus* may still retain the mesocoracoid arch present in *Halec eupterygius* (Text-fig. 62). Another character possibly associated with this general shortening and deepening of the body is the decrease in the number of branchiostegal rays (*Phylactocephalus* has 10, whereas *Halec* has 15 or 16).

Possibly these more advanced features which *Phylactocephalus* possesses indicate a different mode of life. *Halec* could have been benthonic and provided a stock from which a more active pelagic form such as *Phylactocephalus* was derived. Indications of a bottom-dwelling habit are given by the inflection of the lower edge of the mandible (already noticed in the probably benthonic *Eurypholis*, p. 193) and the high number of branchiostegal rays in *Halec*. In *Phylactocephalus* the number of rays is reduced to ten but the jaw still shows signs of being inflected. The overall body shape of *Halec* suggests certain recent benthonic forms such as *Synodus*. However *Synodus* has sub-thoracic pelvics which Marshall (1961 : 368) suggests are used together with the tail as props. Although *Phylactocephalus* has sub-thoracic pelvics, from its shortened, deepened, laterally compressed body it is

more likely to have been pelagic and not benthonic. The forward migration of the pelvics in *Phylactocephalus* would seem to have served a different function to that of *Synodus*, and may possibly be analogous in function to the advanced pelvics of the acanthopterygians. In these the forwardly placed pelvics cancel out the lift force produced by the pectorals when they are used as brakes (Harris 1938 : 37 ; Patterson, 1964 : 452).

The structure of the jaws is identical in *Halec* (Text-fig. 61), *Phylactocephalus* and *Hemisaurida* (Text-fig. 67) providing the most obvious link between the three genera. The premaxillae are simple flattened plates with no articular or ascending processes. The oral border is toothed and forms half of the gape. The maxilla is thin, narrow and elongated, entering the gape behind the premaxilla. The head of the maxilla is little differentiated but does appear to be associated with a small palatine process. The teeth on the maxilla are of characteristic form, larger than those on the premaxilla and inclined forwards. A single, small ornamented supramaxilla is associated with the posterior end of the maxilla.

The dermal upper jaw is unspecialized and primitive but with certain advanced tendencies such as extension beneath the maxilla of the premaxilla, narrowing of the maxilla, and loss of one supramaxilla.

Apart from the jaws the genus *Hemisaurida* (Text-figs. 67 and 68) shows several features not seen in either *Halec* or *Phylactocephalus*. The head and body remain shallow (as in *Halec*) but the snout has become elongated. Coupled with this elongation the jaw articulation has moved forwards to a point below the hind end of the orbit. Thus the suspensorium is inclined forwards. Ventrally the preoperculum in *Hemisaurida* is produced into a prominent backwardly projecting spine (a similar spine has already been noticed in the ichthyotringoid *Apateopholis* Text-fig. 15, but in neither can any functional correlation be attached to it). The pectoral fin, like that of *Halec* and *Phylactocephalus*, is low on the flank, but is characterized by extension of certain of the rays. These extended rays are long and filiform, and the fin is not aliform as in the Exocoetidae or the Cretaceous Chirothricidae (Woodward, 1901 : 281, fig. 10). In both of these latter groups the pectorals are spread into wing-like structures and are positioned quite high on the flanks. The body of *Hemisaurida* is devoid of squamation, whereas both *Halec* and *Phylactocephalus* possess a complete covering of small scales.

Although the caudal skeleton is not well represented in the three genera, sufficient can be made out to indicate that it is comparable (*Halec*, Text-fig. 64 and *Hemisaurida*, Text-fig. 69). The first preural vertebra is fused with the first ural vertebra and this compound centrum supports a stegular dorsally. The second ural centrum is much reduced and appears to support the four hypurals to the upper caudal lobe. The posterior haemal spines have a tendency to become laterally compressed.

A feature of both *Halec* and *Phylactocephalus*, not seen in *Hemisaurida*, is the expanded nature of the bases of the anterior fin rays in all fins except the caudal. These expanded basal regions are ornamented. This feature is not normally associated with soft rays, but is occasionally found on the fin spines of Acanthopterygii.

Little mention has been made in the past of the relationships and systematic position of the halecoids. Agassiz (1834) first used the generic name *Halec*, and also erected the family Halecidae, which he used to include the 'herring-like' fishes, the clupeoids and salmonoids of Cuvier. Pictet (1850) and Davis (1887) retained the family, Davis adding the genus *Phylactocephalus*. Woodward (1901) retained the generic name *Halec* (including *Phylactocephalus* Davis in its synonymy), but put it in the family Enchodontidae, where it has remained to the present day (Bertin & Arambourg, 1958 ; Romer, 1966).

Gregory (1933 : 204) mentioned the genus *Halec* in connection with the Enchodontidae, but pointed out that *Halec* was on a slightly lower level than *Enchodus* in that it possessed well developed maxillary teeth.

Woodward (1901 : 270) also mentioned *Hemisaurida* as an imperfectly defined genus which perhaps belonged in the family Scopelidae. Romer (1966) followed Woodward, but definitely assigned *Hemisaurida* to the family Myctophidae.

Direct relationship with the enchodontoids as constituted in this work can be dismissed because of the following features shown by the Halecidae :

1. Elongate palatine with two rows of teeth.
2. No fenestrated premaxillary pedicel.
3. Supraorbital bone present.
4. Supramaxilla present.
5. Mesocoracoid arch present.

Certain similarities seen in the two groups appear to be the result of convergent modes of life, and possibly similarities in evolutionary potential. These are as follows :

1. A similar neurocranial structure in the loss and reduction of certain bones (orbitosphenoid, basisphenoid, etc.).
2. Reduction in squamation.
3. Trend towards body deepening and shortening.
4. Trend towards snout elongation.
5. Trend for forward migration of the pelvic fins.

The Halecoidei are also in no way related to the Myctophiformes. The incomplete exclusion of the maxilla from the gape, and the absence of ascending and articular processes on the premaxilla completely exclude the halecoids from any connection with the myctophiforms.

The halecoids do, however, show some points of similarity with the myctophiforms which are possibly correlated with convergent and/or parallel evolution, in space as well as time. The halecids occur throughout most of the Upper Cretaceous (Cenomanian, Turonian and Senonian), and this occurrence coincides with the initial radiation of the myctophiforms. Both groups appear to have inhabited similar environments (occurring as fossils at the same horizons), and identical evolutionary forces presumably would have acted upon them. Further, since they were probably derived from a common ancestral stock within the Lower Cretaceous, it is not surprising that some similarities should exist. For example the caudal skeleton

(Text-fig. 64) resembles that of the basal myctophiforms (*Aulopus*, Text-fig. 93 and *Sardiniodes*, Text-fig. 72) in the fusion of preural vertebra one and ural vertebra one. It has already been shown elsewhere that the same state of affairs exists in both the Cimolichthyoidei and the Enchodontoidei. This character then is of no real value in the understanding of relationships. It would appear that the consolidation of the caudal skeleton is general throughout the more basal Protacanthopterygii, and the first step is the fusion of the first preural vertebra with the first ural vertebra.

The nature of the neural components of preural vertebra two (the first free preural vertebra) is of interest. In the halecids the neural spine is complete in *Hemisaurida* but reduced in *Halec*. In the myctophiforms the neural spine is absent. This reduction and loss of the neural spine is probably an expression of the further reduction and consolidation of the caudal skeleton. The basal salmoniforms retain the neural spine on preural vertebra two and in this respect the halecoids are closer to the basal stock.

The Halecoidei as a whole present a constellation of primitive and advanced characters. A similar state of affairs has already been shown in both the Cimolichthyoidei and the Enchodontoidei. These have been placed on a structural grade below that of the myctophiforms and acanthopterygians, due to several primitive characters. The evolutionary trends shown by the halecids agree with those already seen in the cimolichthyoids and enchodontoids and with those in the myctophiforms. These trends are those which align the group within the Protacanthopterygii (*sensu* Greenwood, *et al.*, 1966), and can be summarized as follows :

1. Tendency for premaxilla to exclude maxilla from the oral border.
2. Tendency for supraorbital to be lost.
3. Tendency for supramaxillae to be lost.
4. Reduction in the roof of the post-temporal fossa.
5. Tendency for pelvics to advance.
6. Tendency for the caudal skeleton to become consolidated, the first step being the fusion of preural vertebra one with ural vertebra one.
7. Tendency for the body to become shortened and deepened.

Certain basic features, as opposed to trends, suggest that the halecoids are closest to the salmoniform grade at the base of the Protacanthopterygii. These would include the retention of a mesocoracoid arch ; absence of an ascending process on the premaxilla ; toothed maxilla ; supraorbital present ; numerous branchiostegal rays ; finally the large number of pelvic rays. Following on from these considerations it is apparent that the halecoids are not directly related to any of the above mentioned groups (enchodontoids, cimolichthyoids, myctophiforms or acanthopterygians), but are related only in so far as they are contemporary descendants from an earlier stock within the Salmoniformes.

Order MYCTOPHIFORMES

The ordinal ranking given to this group is based on the fact that it can be separated from the Salmoniformes and the Ctenothrissiformes at least by the opening of the Upper Cretaceous. This is in agreement with the ordinal rank given by Gosline, Marshall and Mead (1966 : 5) although, as these authors point out, there is apparently no one feature that will separate all myctophiforms from all salmoniforms. Greenwood, *et al.* (1966 : 366), using the same criterion, that they could find no diagnostic characters which would satisfactorily distinguish these forms from those they group as the Salmoniformes, therefore consider the Myctophiformes to be merely a suborder within the order Salmoniformes. This ordinal separation will be considered in greater detail further on in this discussion.

The term Myctophiformes is considered preferable to the alternatives previously used, Iniomni and Scopeliformes, since the group has normally been collectively termed the myctophoids.

A re-evaluation of Woodward's (1901 : 235) family Scopelidae, in particular the Cretaceous genera, has shown that several of these do not belong in the Myctophiformes.

Sedenhorstia (*Microcoelia*) White and Moy-Thomas (1941) and *Dactylopogon* von der Marck (1858) are both elopiforms (Goody, 1969).

Ichthyotringa (*Rhinellus*) Cope (1878), and *Apateodus* Woodward (1901), are both primitive salmoniforms (see pp. 169 to 176).

The remaining Cretaceous genera are more nearly referable to the myctophiforms: *Sardiniooides* von der Marck (1858), *Cassandra* (*Leptosomus*) White and Moy-Thomas (1940), *Acrognathus* Agassiz (1843), *Nematonotus* Woodward (1901), and *Sardinius* von der Marck (1858).

Sardiniooides is indisputably a myctophiform and *Cassandra* would appear to be synonymous with it. The species of *Sardiniooides* considered in the systematic account (*Sardiniooides minimus*) was originally described as *Cassandra minima*. This species represents a form very close to the ancestral myctophiform stock. *Sardiniooides* is a genus which has received some attention in the past as being a form from which both the present day Myctophiformes and also possibly the Acanthopterygii could have been derived. Patterson (1964) considered the latter possibility and examined both *Sardiniooides* and *Aulopus* as possible acanthopterygian ancestors. He concluded that they were not on the direct line of descent of the acanthopterygians, but that this ancestry was closer to the Ctenothrissiformes.

A table is given below of the major osteological characters shown by the Salmonoidei (the most primitive group within the Salmoniformes) as illustrated by *Salmo* and the corresponding characters of the Myctophiformes (from *Sardiniooides*) and the Ctenothrissiformes (from *Pattersonichthys*). Similarity to *Salmo* is indicated by a cross (×).

TABLE I

Salmoniformes <i>Salmo</i>	Myctophiformes <i>Sardiniooides</i>	Ctenothrissiformes <i>Pattersonichthys</i>
Parietals meet in mid-line	×	×
Post-temporal fossa roofed	×	×
Orbitosphenoid present	×	×
Basisphenoid present	×	×
No ascending premaxillary process	Prominent ascending process	Small ascending process
Articular premaxillary process present	Prominent articular process	Small articular process
Small, toothed premaxilla	Very long toothed premaxilla	×
Large, toothed maxilla entering the gape	Large, untoothed maxilla excluded from gape	×
2 large supramaxillae	2 reduced supramaxillae	×
Teeth on vomer, palatine, endopterygoid, ectopterygoid	×	×
Supraorbital present	Supraorbital absent	Supraorbital absent
Antorbital present	×	×
Expanded posterior infraorbitals	Unexpanded infraorbitals	Unexpanded infraorbitals
Numerous branchiostegals	9 (numerous in <i>Aulopus</i>)	8 or 9 branchiostegals
Mesocoracoid arch present	Mesocoracoid absent	Mesocoracoid absent
Pectorals low down, 18 rays	Pectorals on flank, 13 rays	Pectorals on flank, 13 rays
3 postcleithra	2 postcleithra	2 postcleithra
Numerous accessory radials	3 or 4 accessory radials	3 or 4 accessory radials
Pelvics abdominal, 13 rays	Pelvics abdominal, 9 rays	Pelvics sub-thoracic, 8-9 rays
Pelvic splint bone present	×	×
Incompletely fused vertebral elements	×	×
Numerous epineurals	×	×
No fin spines	×	2 spinous rays in dorsal
Adipose fin present	×	Adipose fin absent
Stegural present	×	×
2 free ural vertebrae	One free ural vertebra	One free ural vertebra
17 branched caudal rays	×	×
Fulcral scales absent	Fulcral scales present	Fulcral scales present
Cycloid scales on body	Cycloid/ctenoid scales	×
6 hypurals	×	×

The differences noticed between the three groups are all relatively minor ones, and only one factor in the whole list would exclude a direct descent of the two groups from the salmoniforms. This factor is the absence of basal fulcral scales at the base of the caudal fin in *Salmo*. This however is a primitive feature left over from some halecostome ancestor and is lost in later myctophiforms and ctenothrissiforms. Likewise it has presumably been lost in the Recent salmonoids.

The list illustrates the strong basal convergence of three groups which are separated ordinally. It thus would appear that the sardiniod group and the ctenothrissoid group, at the beginning of the Upper Cretaceous, were evolving along similar lines, both having been derived from a common ancestral stock within the salmoniforms.

From the above considerations it can be seen that any division between the three will be somewhat arbitrary. One feature, the presence of a definite ascending process on the premaxilla, separates the myctophiforms and ctenothrissiforms from the salmoniforms. However the ancestral forms from which these arose presumably must have had at least the forerunner of an ascending process. Points for and against ordinal separation can be argued, but in view of the potential within each group, especially the Ctenothrissiformes, it is convenient to give both groups ordinal separation.

Turning to a consideration of the myctophiforms alone, a direct comparison can be made between the Cenomanian *Sardiniodes* and the recent genus *Aulopus*. This latter genus has often been cited in phylogenetic considerations of teleosts (Patterson, 1964), and the skull has been figured by both Woodward, 1902 and Regan, 1911. A complete osteological description has been compiled for comparative purposes and is set out below.

Aulopus filamentosus (Bloch)
(Text-figs. 86–93)

Neurocranium. The neurocranium is shown in dorsal, ventral and lateral views in Text-figures 86, 87 and 88. In general shape the neurocranium is long and broad. The skull-roof is flattened but inclines ventrally in the postero-lateral region. The neurocranium attains its greatest width posteriorly in the region of the pterotics. Much of the skull-roof is formed from the large frontals which are somewhat constricted between the orbits but widen posteriorly. The surface of the frontal is smooth although some surface markings in the form of feeble ridges occur above the curved orbital margin. The sensory canals run within the bone and their course is indicated externally by broad ridges. The frontals meet in a more or less straight suture in the mid-line. Postero-laterally the frontal contacts the sphenotic and pterotic and posteriorly the broad parietal. The tube which contained the supraorbital sensory canal opens postero-laterally above the sphenotic and posteriorly just in front of the parietal. A further posterior branch extends back into the parietal. The tube passes anteriorly, where it receives a further tube from the medial region of the frontal. This medial connection is continuous across the skull-roof (the frontal commissure of Gosline, Marshall & Mead, 1966 : 7). Weitzman (1967 : 527) points out that this cross-connection is a common occurrence in the myctophiforms, but is rare among the salmoniforms. Anteriorly the frontal meets the rear end of the mesethmoid, and just posterior to this the supraorbital sensory canal opens on to the nasal. A prominent supraorbital bone, at the anterior end of the orbit, is attached to the lateral edge of the frontal.

The lateral ethmoid extends from beneath both the frontal and the supraorbital forming the anterior limit of the orbit. It is large and well ossified and attached mainly to the dorsal surface of the parasphenoid. Ventro-laterally the lateral ethmoid is free from the parasphenoid and has a cartilaginous connection with the postero-dorsal region of the palatine. In the mid-line the lateral ethmoids

almost meet one another, and the median laminar orbitosphenoid behind. The edge of the lateral ethmoid has a definite facet for the articulation of the lachrymal.

The nasals are small and elongate with rolled edges resting on the dorsal surfaces of the frontal and mesethmoid. The terminal part of the supraorbital sensory canal passed within a groove on the dorsal surface of the nasal.

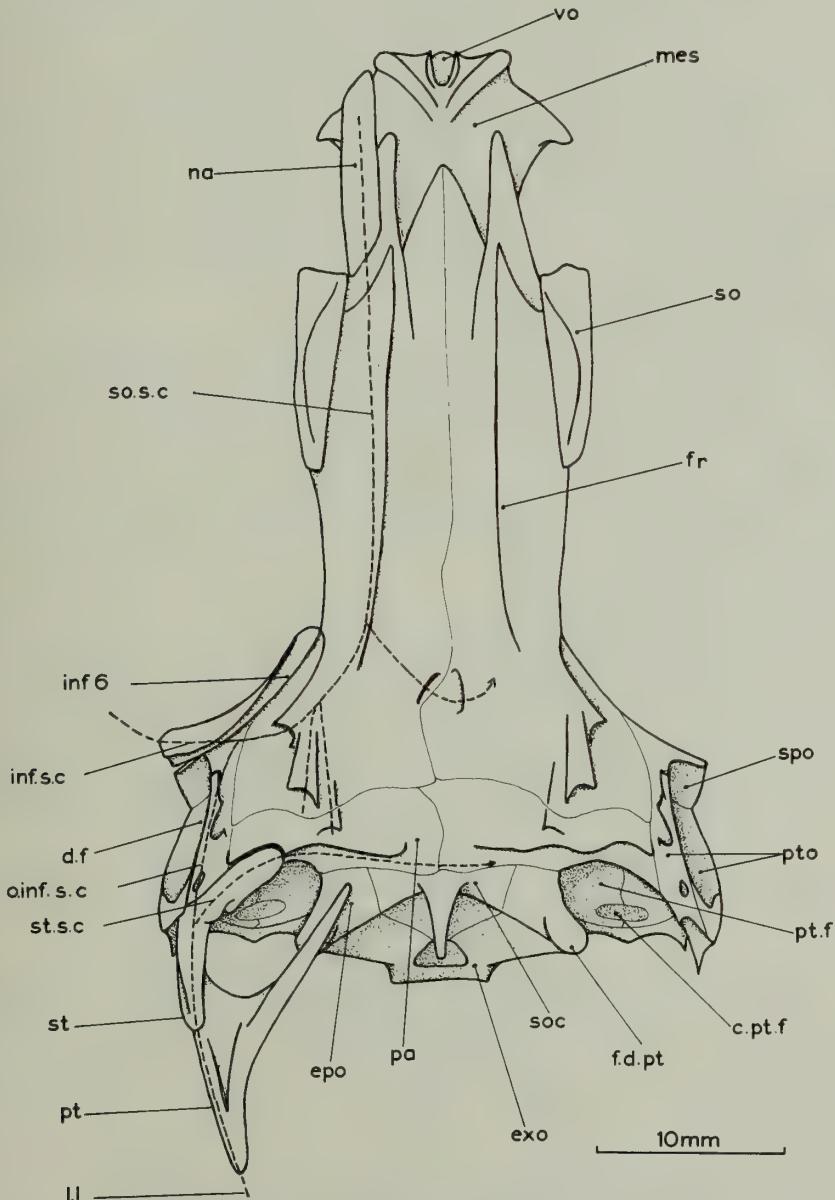


FIG. 86. *Aulopus filamentosus*. Neurocranium in dorsal view. The broken line on the left side of the figure indicates the course of the sensory canals.

The mesethmoid is prominent, extremely well ossified and with its maximum width equalling the interorbital width of the frontals. The mesethmoid is blunt posteriorly where it contacts the frontals, and is hollowed out internally where it is filled with cartilage. Weitzman (1967 : 526) states that *Aulopus* possesses a myodome bone in this region, separate from the ethmoid ossification, also that capsular ethmoid bones appear to be fused to the mesethmoid. The lateral projection of the mesethmoid inclines ventrally to terminate in an articulatory facet. These wings are associated with corresponding, but smaller, projections from the vomer and together provide the articulatory facet for the anterior region of the palatine. Anteriorly the mesethmoid edge has a small median U-shaped indentation which houses a small circular knob of cartilage, presumably the rostral cartilage. Arising from the centre of the bone and passing antero-laterally are two smooth ridges which extend right to the edge. The anterior edge of the mesethmoid between these two ridges provides the articulatory region for the short ascending processes of the premaxilla.

The vomer is attached anteriorly to the ventral surface of the mesethmoid and its internal extensions parallel those of the mesethmoid. Dorso-laterally a facet between the dorsal surface of the vomer and the ventral surface of the mesethmoid contains the articular head of the maxilla. Antero-ventrally the vomer has two oval patches of teeth, on either side of the mid-line, each containing seven or eight small, acutely pointed, recurved teeth. The anterior end of the palatine lies against the lateral vomerine region so that the palatine teeth are continuous with those on the vomer. The vomer is produced posteriorly into a short shaft applied to the ventral surface of the parasphenoid.

The parietals are transversely elongated bones meeting in the mid-line, contacting the frontals anteriorly, the pterotics laterally and the supraoccipital and epiotics posteriorly. The dorsal surface of the parietal, like the frontal, is unornamented except for a low transverse wavy ridge extending from the lateral edge almost to the mid-line. Laterally, the transverse portion of the supratemporal lies on the dorsal surface of the parietal, fitting against the posterior edge of this ridge. More medially the supratemporal sensory canal passed across the parietal behind the ridge. The supraorbital sensory canal terminates posteriorly on the parietal.

The supraoccipital appears on both dorsal and posterior faces of the skull. The small posteriorly directed supraoccipital crest does not extend above the plane of the skull-roof.

The pterotic forms the postero-lateral region of the neurocranium, meeting the sphenotic anteriorly and the frontal and parietal medially in the roof of the post-temporal fossa. A slight crest on the pterotic passes postero-laterally. This crest contains the otic branch of the infraorbital sensory canal which opens midway along the crest, from where it continues in a flanged groove. Postero-medially the supratemporal is closely applied to the pterotic. The extreme posterior end of the pterotic is drawn out into a small acute spine which lies ventral to the longitudinal limb of the supratemporal. The lateral line canal passed through the supratemporal to enter the pterotic posteriorly. The posterior pore in the pterotic for this sensory

canal also transmitted the preopercular sensory canal. Laterally the pterotic is deeply excavated as the dilatator fossa. The anterior part of this fossa is however formed from a postero-dorsal excavation of the sphenotic, and the suture between the pterotic and sphenotic is visible both above and below the fossa.

The post-temporal fossa is large and partially roofed, the roof being composed anteriorly of frontal and posteriorly of parietal and pterotic. The lateral wall and

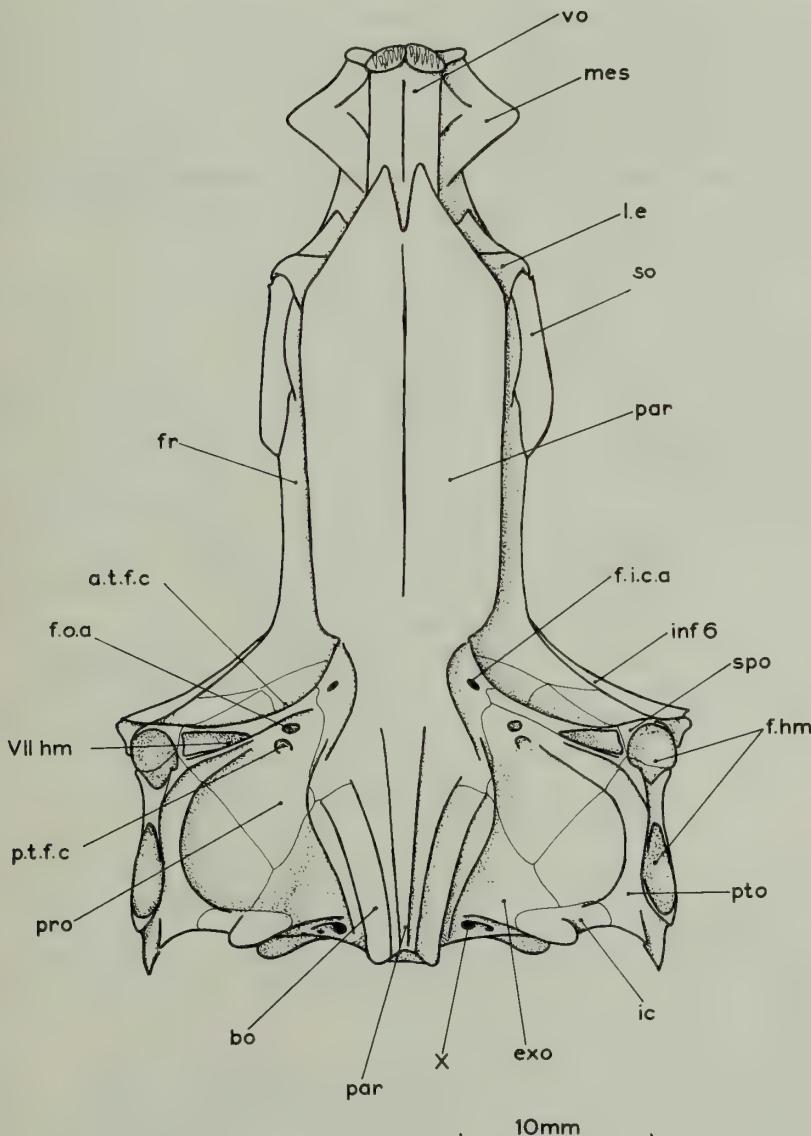


FIG. 87. *Aulopus filamentosus*. Neurocranium in ventral view.

part of the floor are formed of pterotic whilst the medial wall and remainder of the floor consist of frontal, parietal and epiotic. Gosline, Marshall and Mead (1966 : 5) used the presence of a post-temporal fossa in *Aulopus* as evidence for an elopoid derivation of the myctophiforms, believing a post-temporal fossa to be absent in the salmoniforms. As Weitzman (1967 : 528) has indicated this is an erroneous interpretation of the nature of a post-temporal fossa, and post-temporal fossae are present in most salmoniforms. It has been shown in the fossil salmoniform suborders considered in this paper, that the ichthyotringoids and the enchodontoids have representatives with completely roofed fossae, while the cimolichthyoids have a partially roofed fossa. In the floor of the fossa, near to the posterior edge, is a transversely orientated oval fenestra filled with cartilage.

The epiotic joins the supraoccipital medially both on the roof of the skull and on the posterior face. Medial to the opening of the post-temporal fossa the epiotic has a prominent dorsal knob which provides the articulatory area for the dorsal limb of the post-temporal.

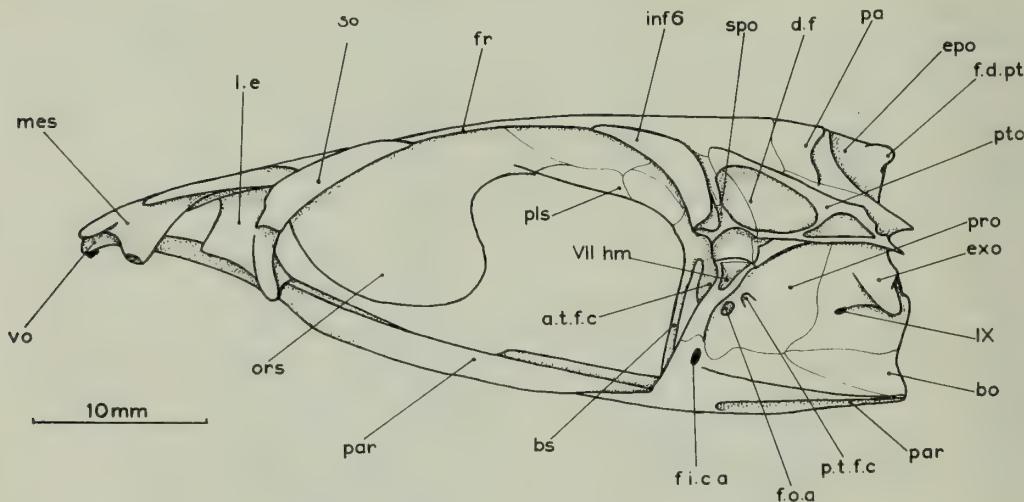


FIG. 88. *Aulopus filamentosus*. Neurocranium in lateral view.

The sphenotic forms the postero-dorsal region of the orbit, contacting the frontal dorsally and the pterotic posteriorly. The sphenotic is partially obscured dorsally by the last infraorbital. This infraorbital is intimately connected to the edges of both the sphenotic and frontal. This intimate connection of the last infraorbital with sphenotic and frontal was noticed in *Sardinioides* (p. 154), and is also seen in *Nematonotus* (Text-fig. 94).

The hyomandibular facet is formed of sphenotic, pterotic and prootic. The upper margin of the facet also forms the ventral border of the dilatator fossa. The facet is in two distinct regions, an anterior cup-shaped depression formed mainly of sphenotic (with a ventral inclusion from the prootic), and a posterior elongated oval cup within the pterotic.

The prootic forms much of the lateral wall of the cranial cavity and myodome as well as a certain part of the posterior wall of the orbit. Ventrally the prootic is thin, meeting the parasphenoid below and the exoccipital behind. More dorsally the prootic divides into two layers, an outer layer inclining dorso-laterally and an inner layer passing medially to form the roof of the posterior myodome. The outer layer contacts the sphenotic in the hyomandibular facet and the pterotic below the mid-region of the same facet.

The lateral region of the cranial cavity below the hyomandibular facet takes the form of a triangular depression. The posterior boundary of the lateral wall of the cranial cavity is formed from a stout strut of bone composed dorsally of pterotic and ventrally of exoccipital. The intercalar is superficial in position and plastered around this strut, covering the suture between the pterotic and exoccipital. The intercalar is, then, an elongated oval bone appearing on both the lateral and posterior faces of the neurocranium.

The inner sheet of prootic contacts its partner in the mid-line to form the prootic bridge separating the myodome from the cranial cavity. The arms of the basisphenoid articulate with the anterior edge of the prootic bridge. The trigemino-facialis chamber is divided by a bony wall into a medial pars ganglionaris and a lateral pars jugularis. The pars jugularis is a short horizontal canal, narrow posteriorly, and lying lateral to the prootic bridge in the angle between the internal and external layers of the prootic. There are two foramina entering the pars jugularis from the pars ganglionaris, arranged one above the other. The ventral foramen is the facial foramen through which passed the hyomandibular branch of the facial nerve. The dorsal foramen is the trigeminal foramen and through this passed the trigeminal, profundus and superficial ophthalmic nerves. The pars jugularis has four external openings ; the posterior one is small, merely transmitting the jugular vein. Dorso-laterally there is an extremely large, elongate foramen reaching up almost to the hyomandibular facet. This foramen directed the hyomandibular nerve upwards and outwards to the hyomandibular. The anterior opening of the pars jugularis is large and triangular, in the hind wall of the orbit. Through it the jugular vein, the orbital artery, the trigeminal, profundus and superficial ophthalmic nerves passed. The orbital artery entered the pars jugularis through the fourth opening which is ventro-lateral in position and close to the posterior opening of the pars jugularis.

The parasphenoid is long and straight, extending for practically the entire length of the neurocranium. The anterior end, lying on the dorsal surface of the vomer, is narrow. Below the lateral ethmoids the parasphenoid is considerably widened, due to the presence of large lateral flanges, inclined slightly ventrally. In the mid-dorsal line of the parasphenoid a thickened pad of bone between the ascending processes provides the attachment region for the basisphenoid pedicel. The ascending processes arise at the level of the basisphenoid pedicel but are not particularly deep and contact the prootics dorsally in the wall of the myodome. Near the base of the ascending process a slight depression marks the articulatory point of the first pharyngobranchial. Above the depression, the foramen of the internal carotid

artery is visible. Posteriorly the parasphenoid articulates with the ventro-lateral edges of the basioccipital, ending posteriorly in two short processes below the hind end of the basioccipital.

The basioccipital, posteriorly, forms the lower part of the occipital condyle and laterally it contacts the exoccipital above and the prootic in front. At the rear end of the lateral face of the basioccipital a pitted depression marks the point of insertion of supracleithral ligaments. Internally the basioccipital forms the posterior walls of the otolith chambers, and also separates them medially. The ventral surface of the basioccipital is deeply concave where it forms the roof to the myodome. The myodome is a deep cone-shaped recess ending blindly at the posterior end of the basioccipital. Ventrally, below the trigemino-facialis chamber, the anterior end of the otolith chamber is formed of prootic and is separated from the myodome by a membranous sheet. The otolith chamber is continued anteriorly as a recess on the internal face of the prootic.

The exoccipitals contact each other in the mid-line of the posterior face of the skull, enclosing the foramen magnum completely. Ventrally each exoccipital contributes to the formation of the occipital condyle. Ventro-laterally the exoccipital is perforated by a large foramen through which the vagus nerve passes. Antero-ventrally the exoccipital contributes to the formation of the wall of the otolith chamber. The exoccipital, near its anterior edge, has a small foramen which transmits the glossopharyngeal nerve. The intercalar is entirely superficial in position, taking no part in the formation of the cranial wall itself. It is wrapped around the postero-ventral corner of the neurocranium beneath the opening of the post-temporal fossa. The intercalar is produced into a thickened knob of bone for the articulation of the ventral limb of the post-temporal.

Ventrally within the orbit the basisphenoid is Y-shaped with a long, incompletely ossified pedicel, and shorter well ossified dorsal arms. These arms attach to the medial edges of the prootic and the anterior edge of the prootic bridge. The orbital face of the prootic contains the large anterior opening of the pars jugularis. Medial to this opening a further small foramen is visible which transmits the oculomotor nerve. Dorso-laterally the prootic meets the sphenotic and dorso-medially the pleurosphenoid. The pleurosphenoids are separated in the mid-line by a small optic fenestra, bordered ventrally only by the basisphenoid. A slight groove extends from the anterior opening of the pars jugularis to pass dorsally across the face of the pleurosphenoid. This groove indicates the course of the superficial ophthalmic nerves towards the ventral surface of the frontal.

The orbitosphenoid is large, flattened and in the anterior orbital region. Ventrally it almost meets the parasphenoid and anteriorly the lateral ethmoids. Posteriorly the orbitosphenoid contacts the pleurosphenoids.

Circumorbital series. There are eight circumorbital bones, of which seven are associated with the infraorbital sensory canal. The eighth is the supraorbital which is not canal bearing. The antorbital is a small fragile slip of bone contacting the supraorbital postero-dorsally, and the lachrymal antero-ventrally. The lachrymal is the largest bone in the series and overlaps the upper regions of the maxilla.

The infraorbital sensory canal runs within a tube in the lachrymal and an antero-dorsal opening passed the sensory canal to the antorbital. The lachrymal extends back to the centre of the orbit where it becomes shallower. The remainder of the circumorbital ring is composed of five unexpanded infraorbitals, each bearing a flanged groove for the infraorbital sensory canal.

Hyopalatine bones. The hyopalatine bones are shown in medial view in Text-figure 89. The hyomandibular is neither deep nor broad. The head of the bone is double and the two condyles are connected by a thin lamella of bone. The opercular process is large and extends postero-ventrally. The lateral face of the hyomandibular has a shallow crest arising from the anterior head region and curving postero-ventrally to run along the posterior edge of the bone. This crest disappears near the ventral end of the hyomandibular. The upper region of the preoperculum lies against the posterior edge of this crest. Ventrally the hyomandibular tapers and is terminated by cartilage. The anterior region is thin and overlain ventrally by the postero-dorsal edge of the metapterygoid. The hyomandibular branch of the facial nerve enters the bone through a small foramen close to the anterior region of the head. Within the bone the nerve divides and the opercular nerve passes through a foramen on the posterior edge of the bone while the hyoidean and mandibular branches leave through a larger foramen in the angle between the opercular process and the crest on the lateral face of the bone.

The symplectic is long, thin and narrow and forwardly inclined. Its connection with the hyomandibular is cartilaginous and the interhyal also contacts this cartilage

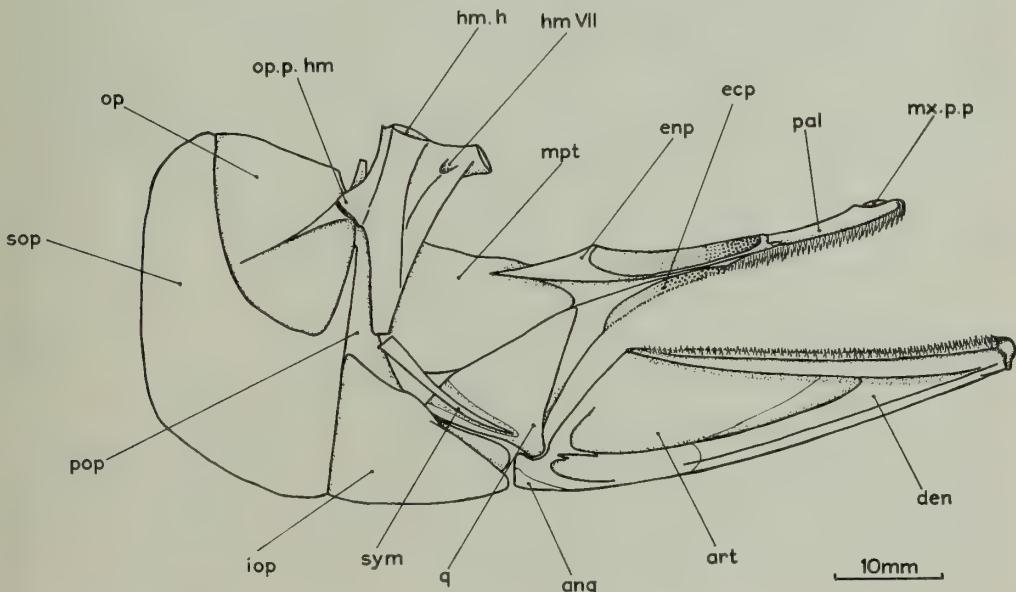


FIG. 89. *Aulopus filamentosus*. Hyopalatine and opercular bones and mandible of the left side in medial view.

block. The symplectic is acutely pointed ventrally and lies in a medial groove on the quadrate.

The quadrate is large and triangular with a transverse condyle. The bone is thin but its anterior and posterior edges are slightly thickened. The symplectic groove is long and shallow, ending ventrally just behind the condyle. The posterior thickened edge is grooved slightly for the leading edge of the preoperculum. The anterior edge of the quadrate is sutured to the ectopterygoid.

The ectopterygoid is bent through a slight angle. Anteriorly it meets the palatine in an elongate oblique suture, and in its anterior half bears an elongate, ventral tooth patch. The individual teeth are minute, especially posteriorly. The dorsal edge of the ectopterygoid is grooved for the reception of the endopterygoid.

The metapterygoid is a well ossified, thin sheet of bone contacting the quadrate ventrally. More dorsally the metapterygoid has a prominent internal horizontal flange widening anteriorly. The posterior region of the endopterygoid is inserted on to the ventral surface of the anterior part of this flange. Postero-dorsally the metapterygoid overlies the antero-ventral part of the lateral face of the hyomandibular.

The endopterygoid is thin and horizontal. The dorsal surface is slightly concave and articulates medially with the ventral surface of the lateral parasphenoid flange. The endopterygoid bears an oval patch of teeth ventrally. As on the ectopterygoid the teeth are minute and give the appearance of being nothing more than a roughened surface.

The palatine is elongate and thicker than the ectopterygoid, inclining, anteriorly, towards the mid-line. Postero-dorsally the palatine is thickened medially where it connects with the ventro-lateral region of the lateral ethmoid. The maxillary process of the palatine is hollow and filled with cartilage. Gosline, Marshall and Mead (1966 : 2) have suggested that the palatine bone, in respect of its articulation with the maxilla, is different from the salmoniforms. It certainly is significantly different from that of the elopoids (Gosline, Marshall and Mead, 1966, fig. 1; Goody, 1969), but Weitzman (1967 : 528) points out that many salmoniforms have the same arrangement as in the myctophiforms. On the medial face of the maxillary process the lateral wing of the mesethmoid attaches. Below the maxillary process is a further facet for the reception of the lateral vomerine wing. Ventrally the palatine has a broad band of teeth. The teeth are of two main types, minute marginal teeth continuous with those on the ectopterygoid, and larger, acutely pointed teeth in two rows. The tooth bearing region tapers posteriorly so that at the extreme posterior end only the internal row of palatine teeth remains.

Dermal upper jaw. The dermal upper jaw is shown in lateral view in Text-figure 90. The premaxilla is long and narrow for most of its length, forming the entire oral border of the mouth. Anteriorly a short broad ascending process meets its partner in the mid-line and both rest on the anterior edge of the mesethmoid. The internal face of the ascending process is hollowed out and rests on cartilage above the vomerine region. From the postero-lateral edge of the ascending process there is a short, stout articular process. The premaxilla is furnished with minute marginal

teeth. Anteriorly the teeth are arranged into three distinct rows, a minute row of marginal teeth, a median row of slightly larger teeth and an internal row of much larger teeth. All of the teeth are similar, being long, thin, needle-like and slightly recurved. Posteriorly the teeth decrease in size and are confined to two rather than three rows.

The anterior part of the maxilla, like that of the premaxilla, is inclined medially. The dorsal surface of the anterior part of the bone is excavated as a shallow depression into which the maxillary process of the palatine fits. The actual head of the maxilla is small and rounded, sandwiched between the dorsal surface of the vomer and the ventral surface of the antero-lateral mesethmoid projection. The articular process of the premaxilla fits against a shallow concave facet on the anterior edge of the maxilla just lateral to the maxillary head. The maxilla is an elongate shaft of bone, stout anteriorly but becoming flattened and deepened posteriorly. The lateral face is smooth and dorsally supports two supramaxillae. Both supramaxillae are small and elongate, the anterior one being the smaller.

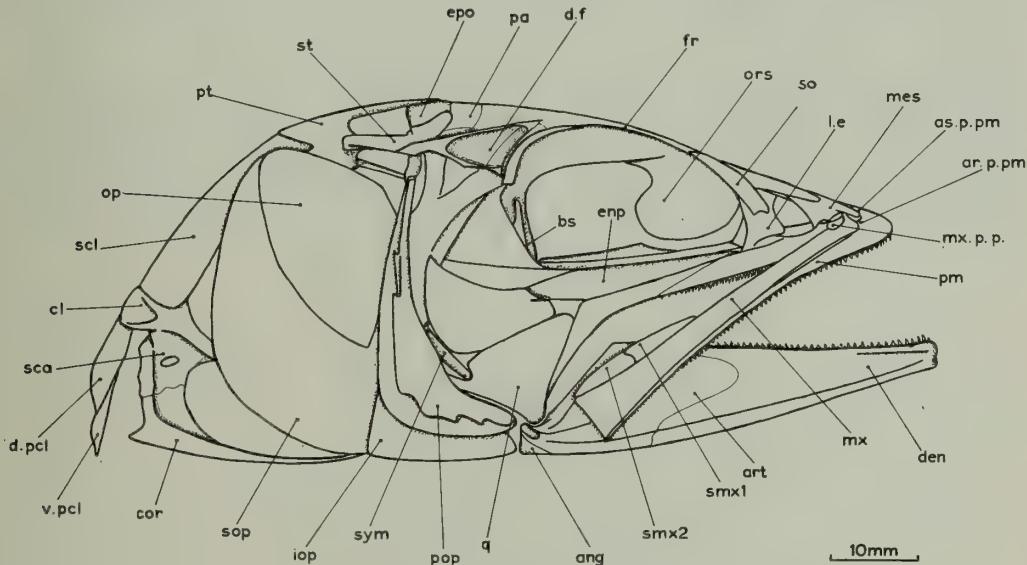


FIG. 90. *Aulopus filamentosus*. Skull in lateral view.

Mandible. The mandible is shown in medial and lateral views in Text-figures 89 and 90. It is long and deepened posteriorly. The dentary forms the greater part of the ventral border, the whole of the oral border and a considerable proportion of the lateral face. In lateral view the dentary is V-shaped with the indentation occluded by the anterior part of the articular. The symphysis is constricted and blunt and each mandible has an inflected ventral edge. Ventro-laterally a tube within the bone opens to the exterior by a row of small pores. The mandibular sensory canal runs within the tube. Posteriorly the ventral limb of the dentary

meets the articular in a straight suture. The upper limb of the dentary forms the tooth bearing margin of the jaw, the teeth being borne on a stout medially directed flange. The teeth are present in three major rows and are similar to those on the upper jaw.

The articular forms the posterior jaw region and has a shallow, concave, transversely arranged facet. The articular is produced behind the facet into a small retroarticular process. The mandibular sensory canal runs within the articular and opens on to the surface through several pores. The dorsal part of the articular is thin although the posterior edge is thickened.

The angular is a small knob of bone applied to the extreme postero-ventral surface of the articular.

Opercular bones. The opercular bones are shown in medial and lateral view in Text-figures 89 and 90. The operculum is reduced in extent whereas the suboperculum is greatly expanded. The operculum has straight anterior and dorsal edges, but is rounded posteriorly. The lateral face of the bone is completely smooth. The opercular facet is prominent, and near to the dorsal end of the anterior edge of the operculum. The facet is supported by an oblique flange crossing the internal face of the operculum.

The suboperculum is greatly expanded forming the entire posterior edge of the opercular cover. Its dorsal border lies medial to the ventral and posterior edges of the operculum, and a large pointed process from the antero-dorsal corner extends upwards medial to the operculum. The anterior edge of the suboperculum is thickened and overlaps the posterior edge of the interoperculum medially.

The interoperculum is roughly triangular with a vertical posterior edge. It ends anteriorly just behind the angular region of the mandible.

The preoperculum is large and curved forwards ventrally. The dorsal termination of the preoperculum lies immediately above the opercular process. Dorsally the leading edge rests against the hyomandibular crest, but below the crest the edge of the preoperculum expands anteriorly to overlap the lateral face of the ventral end of the hyomandibular. Ventrally the preoperculum lies against the posterior edge of the quadrate. The preopercular sensory canal runs within a tube in the centre of the lateral face of the preoperculum, and gives off large posteriorly directed pores for subsidiary branches of the canal. The extreme posterior edge of the preoperculum lies over the anterior edges of both the operculum and suboperculum, and covers much of the interoperculum. On the ventral part of the preoperculum the sensory canal tube opens by three large pores. The anteriormost opening is directly behind the retroarticular process of the mandible.

Hyoid arch and branchiostegal rays. The hyoid arch consists anteriorly of a large ventral hypohyal and a smaller dorsal hypohyal connected to it by cartilage. The ceratohyal is long and shallow, whereas the epihyal is shorter and triangular. A small mesially constricted interhyal connects the epihyal to the interspace of cartilage at the base of the hyomandibular. Both the ceratohyal and the epihyal have a continuous groove on their lateral faces for the hyoidean artery. A median, vertically arranged urohyal extends posteriorly from its connection with the ventral

hypohyals. Fifteen branchiostegal rays occur on the hyoid arch, all being of similar size and shape. Eight are present on the ceratohyal and 7 on the epihyal.

Branchial arches. The basibranchials are fused into a single median elongate element, supporting three pairs of hypobranchials. Five discrete ceratobranchials are present, the first two of which bear toothed gill-rakers. Gill-rakers are absent on the third and fourth ceratobranchials but teeth are still present. The fifth ceratobranchial is the only remaining ossification of the fifth arch. It is enlarged into a prominent tooth plate, the inferior pharyngeal bone. Weitzman (1967 : 530) finds a small cartilaginous fifth epibranchial, ligamentously attached to the fifth ceratobranchial. Four epibranchials are present and, like the ceratobranchials, the first two bear toothed gill-rakers but the third and fourth simply bear teeth. There are four pharyngobranchials ; the first is small and attaches to the parasphenoid. Pharyngobranchials 2, 3 and 4 are fused into a tooth plate which opposes the inferior pharyngeal bone. Weitzman (1967 : 530) reports that a fifth pharyngeal tooth plate occurs in *Aulopus*, but he goes on to suggest that by its morphological relationships this tooth plate may actually belong to the fourth arch. Nelson (1967 : 286) indicates that *Aulopus* has a fifth tooth plate as a separate element.

Pectoral girdle and fin. The pectoral girdle is shown in medial view in Text-figure 91. The supratemporal is composed of transverse and longitudinal limbs. The transverse limb lies on the postero-dorsal regions of both the pterotic and parietal forming a part of the roof of the post-temporal fossa (Text-fig. 86). This extension contains the supratemporal sensory canal. The longitudinal limb is the shorter of

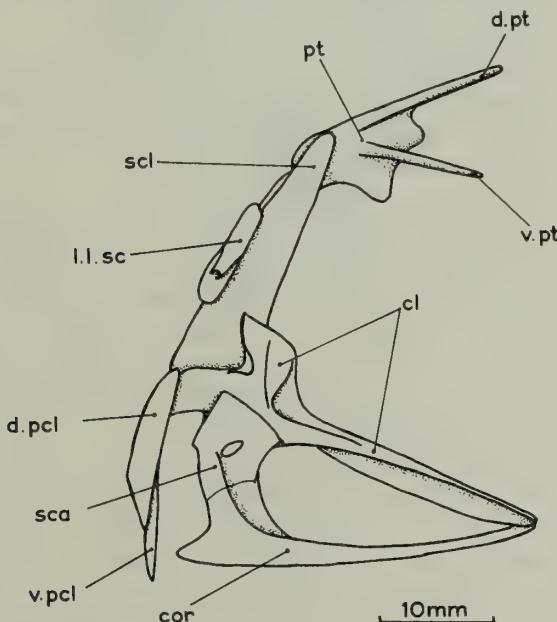


FIG. 91. *Aulopus filamentosus*. Pectoral girdle of the left side in medial view.

the two. The posterior part of the longitudinal limb receives the lateral line sensory canal from the post-temporal. The sensory canal divides within the supratemporal and the supratemporal commissure passes medially whilst the main branch extends anteriorly. The post-temporal has an elongated strut-like dorsal limb articulating with the dorsal surface of the epiotic, and a shorter, unexpanded ventral limb articulating with the intercalar. A large flange unites the two limbs posteriorly and forms a medial facet for the articulation of the supracleithrum. The lateral line canal enters the post-temporal through a foramen in the anterior region of the supracleithral facet and the canal passes through the bone to open antero-laterally.

The supracleithrum is large, flattened and broad with a thickened anterior edge. The lateral line canal enters the bone mid-way down the posterior edge. The blunt ventral end of the supracleithrum articulates with the lateral face of the cleithrum.

The cleithrum is unusual in that it has no noticeable dorsal extent above the attachment of the endoskeletal girdle. (This character is also noticed in other myctophiforms, e.g. *Chlorophthalmus*.) The posterior part of the cleithrum forms a small plate-like expansion ornamented with a V-shaped groove on its lateral face. The dorsal postcleithrum attaches to the internal face of this posterior extension. Ventrally the cleithrum extends anteriorly and is unexpanded but the anterior edge inclines medially. The endoskeletal girdle attaches to an internal flange from the cleithrum.

The scapula is a small, roughly rectangular bone, thin for the most part, but with a thickened posterior edge. It joins the internal cleithral flange dorsally and the coracoid ventrally. A large oval foramen is present in the central region of the scapula. On the thickened posterior edge of the scapula there is a smooth saddle-shaped facet for the articulation of the anteriormost fin ray.

Ventrally the coracoid is produced into a long slender process which contacts the anteriormost tip of the cleithrum. A large fenestra is left between the coracoid and the cleithrum. The postero-ventral tip of the coracoid projects back as a short pointed process below the fin insertion.

Two postcleithra are present, the larger dorsal one has a thickened anterior edge but is thinner and rounded posteriorly. The ventral postcleithrum is a small slip of bone attached to the antero-ventral edge of the dorsal postcleithrum.

The pectoral fin consists of 13 rays, all of which are segmented distally. The first ray is the longest and both it and the second ray are unbranched, but the remainder of the rays are branched. The rays are supported by four radials which contact the thickened posterior edge of the scapula and the scapulo-coracoid suture. The radials are hourglass shaped and increase in size ventrally.

Pelvic girdle and fin. The pelvic girdle is made up of two pelvic bones connected in the mid-ventral line. Each bone is large with a considerable horizontal extent, tapering anteriorly to a point. The fin is inserted on a thickened postero-lateral condyle which is merely a continuation of the posterior edge of the bone. The condyle is supported by a lateral strengthening ridge. The medial part of the posterior edge of the bone, internal to the insertion of the last pelvic ray, is drawn out posteriorly into a very long, narrow, blunt posterior process. Weitzman (1967 :

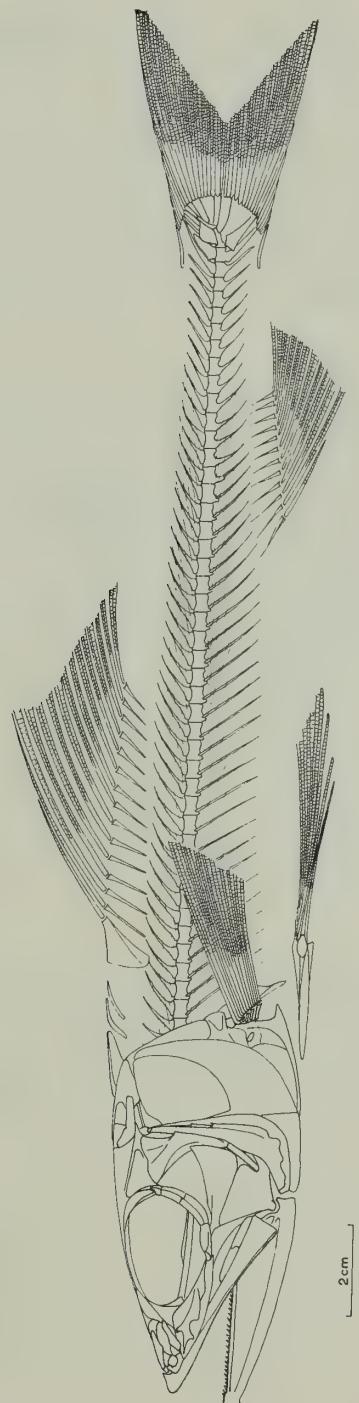


FIG. 92. *Autolopus filamentosus*. Skeleton, scales omitted.

513, fig. 6) shows the pelvic girdle of *Salmo* and illustrates small posterior cartilaginous processes from the 'ischial plate'. These processes obviously correspond to the large ossified processes of *Aulopus*.

The pelvic fin is composed of 9 rays all of which are segmented distally. The first ray is unbranched, the next three are simply bifurcated whereas the remaining five rays are normally branched. Gosline, Marshall and Mead (1966 : 5, fig. 3) have noticed the fusion of the ventral half of the innermost pelvic ray with the inner radial element. Like the structure of the palatine bone, however, this feature is of variable occurrence in both salmoniforms and myctophiforms. Also it is a feature which is not easily seen in fossil forms and as such has been left out of consideration here.

Vertebral column. The vertebral column is shown in the restoration, Text-figure 92. It consists of 50 vertebrae, of which 14 are caudal. The centra are small, slightly longer than deep and mesially constricted. Each precaudal centrum bears a pair of small ventro-lateral transverse processes. These gradually increase in length towards the posterior end of the precaudal region. The transverse processes support thin, needle-like pleural ribs which are longest anteriorly but decrease in size posteriorly. The first precaudal vertebra articulating with the occipital condyle does not possess either transverse processes or pleural ribs. The neural arches along the entire length of the column are well ossified and intimately connected with the centra. The neural spines arise towards the posterior end of each arch. The neural spine of the first vertebra has become fused with the first accessory radial to produce an expanded plate of bone extending upwards in the mid-dorsal line. This plate extends back and tapers to end above the fifth precaudal vertebra. Two or three additional, unexpanded accessory radials occur posterior to the first and are ligamentously attached to the neural spines of precaudal vertebrae 3, 4 and 5. Prezygapophyses and postzygapophyses occur throughout the column but are never particularly prominent. Epineurals and epipleurals are associated with the precaudal vertebrae.

Median fins and tail. The median fins are shown in the restoration, Text-figure 92. The dorsal fin is in the second quarter of the back and consists of 16 rays. None of the rays is excessively elongate, the longest being the second and third. The first ray is the shortest and is unbranched, the longer second one is also unbranched. All of the rays are segmented. The dorsal fin radials are long and thin except for the anteriormost one which is expanded into an anterior keel-like structure.

The anal fin occurs towards the posterior end of the body, well behind the dorsal fin. Eleven rays are present and again none is excessively elongate. The third and fourth rays are the longest. The first three rays are unbranched. None of the radials is expanded.

An adipose fin without any skeletal components is positioned above the centre of the anal fin.

The caudal skeleton (Text-fig. 93) is composed of five vertebrae : two free preural vertebrae (preurals 2 and 3) ; one fused vertebra (preural 1 and ural 1) ; and

a terminal half-centrum (ural vertebra 2). Preural vertebrae 2 and 3 both bear haemal spines which are slightly expanded and support the hypaxial accessory caudal rays. Only preural vertebra 3 bears a neural spine, preural vertebra 2 merely supports an expanded neural arch. The fused vertebra (preural 1 and ural 1) bears the parhypural (haemal spine of preural one) and the first two hypural bones ventrally. The centrum itself is slightly upturned. The parhypural is expanded and only has a small area of attachment with the centrum and anteriorly overlaps the haemal spine of preural vertebra 2. Hypurals 1 and 2 are sutured together, with hypural 1 being the larger. The terminal half-centrum bears a series of four hypurals supporting the upper fin rays. The stegural is borne on the dorsal

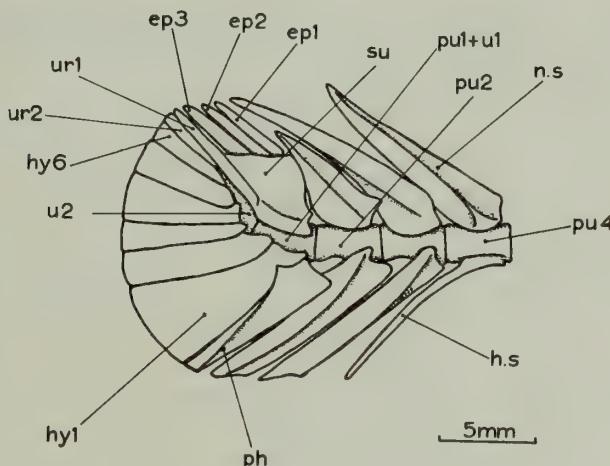


FIG. 93. *Aulopus filamentosus*. Caudal fin skeleton in lateral view.

surface of the fused centrum and consists of an elongate postero-dorsally directed strut, with an elongated expansion anteriorly. A second and possibly a third uroneurals, both rod-like, occur postero-dorsally immediately behind the stegural. Three epurals are associated with the dorsal edge of the stegural.

Nineteen principal caudal rays are present of which 17 are branched. Accessory rays are present epaxially and hypaxially, there being 16 in all. In front of the accessory rays a single large flattened fulcral scale is present above and below the peduncle.

Scales. The entire body is covered with a uniform coat of regularly shaped, feebly ctenoid scales. The lateral line scales are slightly enlarged and bear a median ridge. In the head region the scales extend on to the cheek and the posterior end of the mandible. Scales also cover the rear end of the skull-roof as far as the parietals, and the anterior and posterior edges of the preoperculum, operculum and suboperculum.

The genus *Aulopus* described in the preceding pages represents the most primitive living representative of the Myctophiformes and many comparable features can be seen in the Cretaceous *Sardinioides*. The similarities can conveniently be listed :

1. Neurocranium shallow with a roofed post-temporal fossa.
2. Parietals in contact along the mid-dorsal line.
3. Both orbitosphenoid and basisphenoid present.
4. Antorbital present.
5. Two supramaxillae present, although somewhat reduced in extent.
6. Maxilla long and narrow except posteriorly where it is deepened.
7. Premaxilla with ascending and articular processes and a very long alveolar arm.
8. Supratemporal present above the opening to the post-temporal fossa.
9. Pectoral fin on the flank, the girdle having lost the mesocoracoid arch.
10. Pelvic fin composed of 9 rays.
11. In the caudal skeleton preural vertebra one is fused with ural vertebra one.
12. Ural vertebra two present as a small half-centrum.
13. An adipose fin present (seen in *Sardinioides monasteri* from Sendenhorst, Westphalia).
14. Basal fulcral scales present both above and below the caudal peduncle.
15. Fin spines absent.
16. Three or four accessory radials (interneurals) between the occiput and the dorsal fin.
17. Epineurals present on all of the precaudal vertebrae and epipleurals present in abundance.
18. Body scaling extends on to the opercular bones and certain of the head bones.

These numerous similarities in overall construction represent the basic characters of the myctophiforms, the differences being few in number and of only minor significance. Firstly, *Sardinioides* has a narrow parasphenoid below the orbit, but in *Aulopus* the parasphenoid is greatly expanded. The supraorbital bone would appear to be absent in *Sardinioides* but is large and forms part of the orbital border in *Aulopus*. However it may be that what is termed an antorbital in the description of *Sardinioides minimus* (see p. 154) is a supraorbital. The ascending process of the premaxilla differs somewhat ; in *Sardinioides* (Text-fig. 70) it is long, but in *Aulopus* (Text-fig. 90) it is considerably reduced and rounded. In *Sardinioides* the suboperculum is little expanded and the operculum is large, whereas in *Aulopus* the suboperculum has greatly expanded dorsally to form the whole posterior edge of the opercular cover, the operculum consequently having become greatly reduced. The pelvic fins, although possessing the same number of rays in both genera, are abdominal in position in *Sardinioides* (Text-fig. 71) but seem to have migrated to a sub-thoracic position in *Aulopus* (Text-fig. 92). *Sardinioides* has a pelvic splint bone (Gosline, 1961 : 18) on the outer surface of the dorsal half of the

first pelvic ray, but this structure is absent in *Aulopus*. The branchiostegal ray number is variable. There are 8 or 9 rays in *Sardiniooides*, but *Aulopus* has approximately 15. The vertebral column is a variable feature in that the elements are incompletely fused in *Sardiniooides* but are much more closely united in *Aulopus*. Although the total vertebral count is different (30 in *Sardiniooides*, 50 in *Aulopus*), the number of caudal vertebrae is very similar, with 16 in *Sardiniooides* and 14 in *Aulopus*. Both genera have feebly ctenoid scales, but in *Sardiniooides* cycloid scales are also present. Although the basic composition of the caudal skeleton is the same in the two genera, that of *Sardiniooides* (Text-fig. 72) has a fairly wide gap between the second and third hypurals, whereas in *Aulopus* (Text-fig. 93) hypurals two and three contact each other.

These differences are only minor ones and the two genera are extremely closely related although being considerably separated in time. It is difficult to derive *Aulopus* directly from *Sardiniooides* because of the possible absence of a supraorbital, the small number of branchiostegal rays and the presence of a gap between the second and third hypurals in *Sardiniooides*. The hypural gap is also seen in the Ctenothrissiformes (Text-fig. 77), in certain polymixioid beryciforms (Patterson, 1968b), and in the Paracanthopterygii (*sensu* Greenwood, *et al.*, 1966). No obvious functional significance can be attached to this feature, the fin outline remaining the same irrespective of whether the gap is present or absent. Many of the more advanced myctophiforms exhibit a slight gap but never to the extent shown in *Sardiniooides*. If this is in fact a variable feature, then it would not on its own exclude *Sardiniooides* from the ancestry of *Aulopus*.

Thus it would appear that *Sardiniooides* although not directly ancestral to *Aulopus* is extremely close to this ancestry. Both genera represent equivalent basal forms from which most, if not all, of the present day myctophiforms can be derived.

The two genera *Acrognathus* and *Nematonotus* which were included in Woodward's (1901) family Scopelidae both show strong affinities with the myctophiforms. The skull-roof of an undetermined species of *Nematonotus* (B.M.N.H. specimen P.48681) is shown in Text-figure 94, and it is very similar to those of both *Sardiniooides* and *Aulopus* (Text-fig. 86). Apart from the skull-roof there are certain minor differences. The head and body of *Nematonotus* (Text-fig. 95, *Nematonotus bottae*) are somewhat deeper than in *Sardiniooides*, and the premaxilla has a very long ascending process and a large articular process. One major difference occurs and this concerns the maxilla which in *Nematonotus* enters the gape behind the premaxilla, a feature not seen in any myctophiforms, and the maxilla is toothed. Corresponding to the entry of the maxilla into the gape, the bone itself is deeper and supports two supramaxillae which are considerably larger than those in *Sardiniooides*. Like *Aulopus*, but unlike *Sardiniooides*, there is no gap between the second and third hypurals. The base of the first uroneural is forked in *Nematonotus bottae* (Text-fig. 96), this being a primitive feature seen in such forms as *Elops* (Text-fig. 80) and to a very slight extent in *Salmo* (Text-fig. 81), but in neither *Sardiniooides* nor *Aulopus* (see also Patterson, 1968a : 226).

The major feature in which *Nematonotus* differs from the myctophiforms is the toothed maxilla. Its upper jaw is intermediate in form between the myctophiform *Sardinioides* and the ctenothrissiform *Pattersonichthys*. On this basis the genus *Nematonotus* cannot be satisfactorily included within the Myctophiformes and

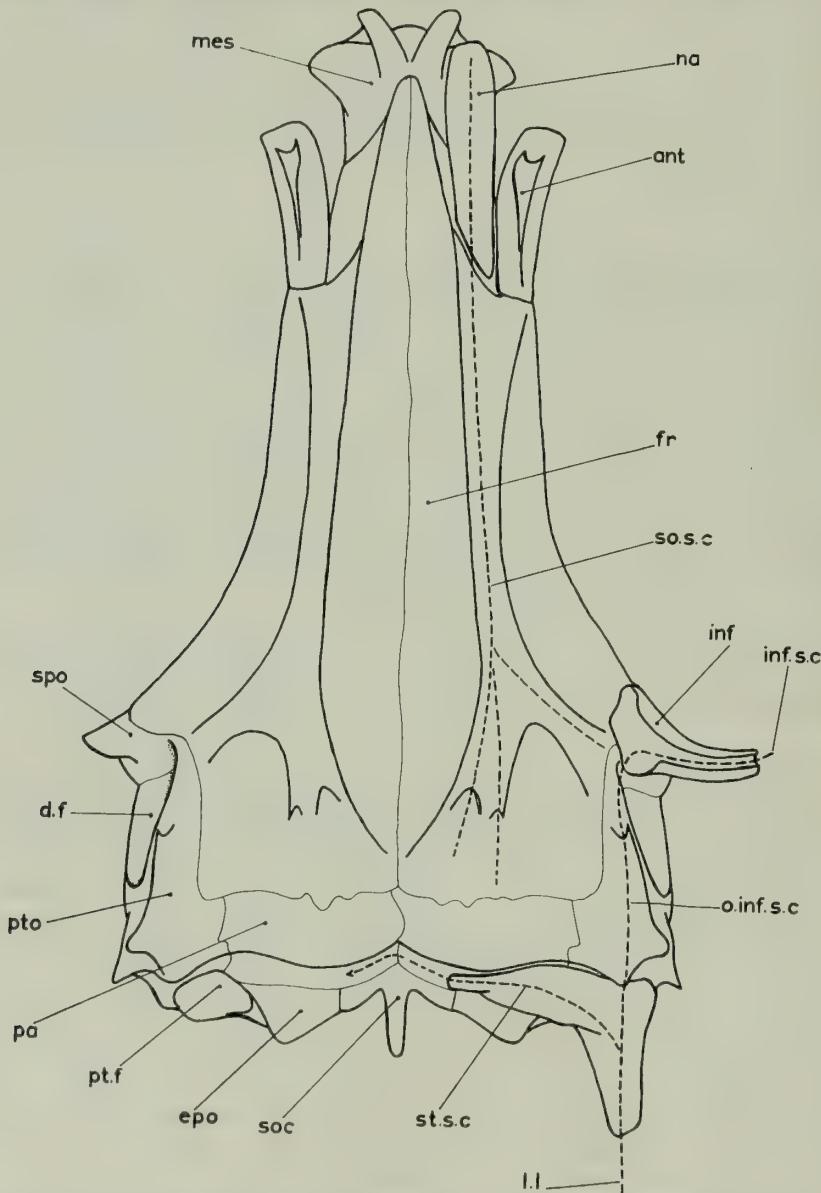


FIG. 94. *Nematonotus* sp. Neurocranium in dorsal view. The broken line on the right side of the figure indicates the course of the sensory canals. From B.M.N.H. number P.48681. Middle Cenomanian, Hajula, Lebanon.

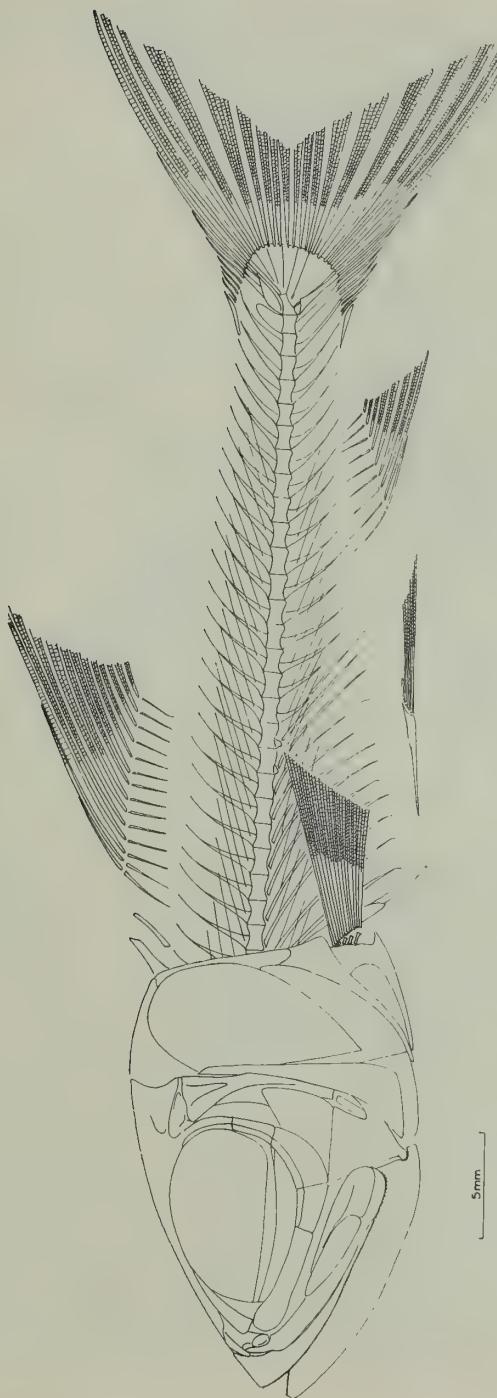


FIG. 95. *Nematomotus bottae* (Davis). Restoration of the skeleton, scales omitted.

because of its abdominal pelvic fins cannot be included within the Ctenothrissiformes. Thus *Nematonotus* emphasizes the basal convergence of the ctenothrissiform and myctophiform lineages, and for the time being is best included in the Salmoniformes as a separate suborder, Nematonotoidei.

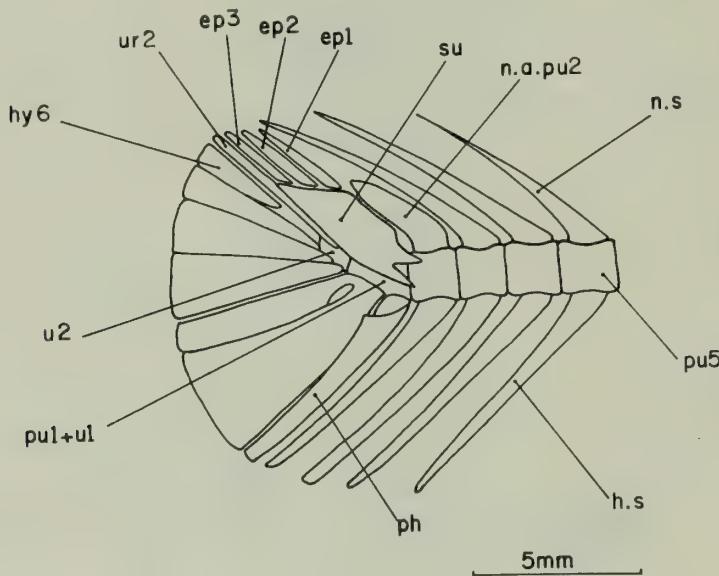


FIG. 96. *Nematnotus bottae* (Davis). Caudal fin skeleton in lateral view.

A further genus considered by Woodward (1901) to be a myctophiform is *Acrognathus*. In many respects this resembles *Sardiniooides*, notably in respect of the caudal skeleton, but the maxilla, although apparently untoothed, is expanded posteriorly and enters the gape behind the premaxilla. The maxilla also supports two large supramaxillae. The large size of the basal fulcral scales recalls *Sardiniooides* and *Aulopus*, but not the Ctenothrissiformes in which the fulcral scales are reduced. An adipose fin could not be made out in *Acrognathus* but the pelvic fins are abdominal. Perhaps *Acrognathus* is best included with *Nematonotus* in the suborder Nematonotoidei, which lies very close to the group from which both the Myctophiformes and the Ctenothrissiformes were derived.

The last of the Cretaceous genera considered by Woodward (1901) to be a scopeloid is *Sardinius*. The species *Sardinius cordieri* von der Marck (Text-fig. 97) certainly shows several myctophiform characters which are comparable with *Sardiniooides* and *Aulopus*. For instance the maxilla is excluded from the gape, the ascending process is abbreviated (as in *Aulopus*), the suboperculum is large and the operculum is small, preural vertebra one is fused with ural vertebra one in the caudal skeleton, and the neurocranium is shallow.

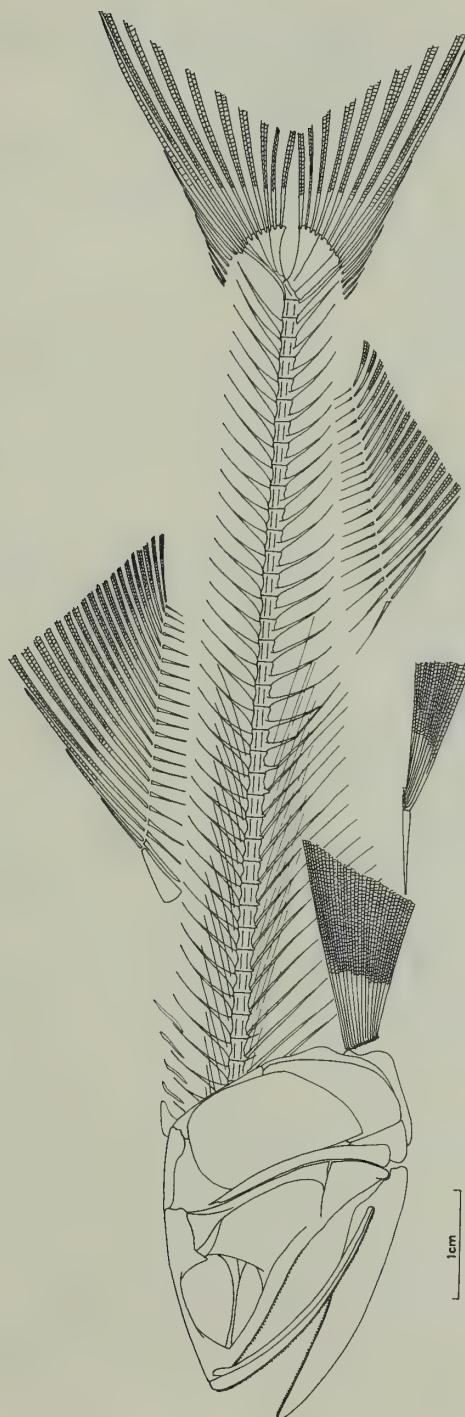


FIG. 97. *Sardininius cordieri* von der Marck. Restoration of the skeleton, scales omitted.

Certain features shown by *Sardininius* would appear to be in a less advanced condition than those shown in the *Sardiniooides-Aulopus* complex, and yet others appear to be more advanced. The more primitive features are :

1. Pectoral fin low on flank with as many as 22 rays.
2. Pelvic fins abdominal with 11 rays.
3. Five or six accessory radials present in advance of the dorsal fin.

The more advanced features are :

1. No posterior expansion of the maxilla.
2. No supramaxillae.
3. Much widened gape with the jaw articulation positioned posterior to the occiput.
4. No fulcral scales at the base of the tail.
5. No pelvic splint bones.
6. Markedly ctenoid scales.

Sardininius from the above considerations seems to have been possibly an early offshoot from either the myctophiform lineage or the group of Salmoniformes from which the Myctophiformes were derived. It is obviously much closer to the myctophiforms than to any of the other salmoniform groups so far considered, e.g. enchodontoids, halecoids. The evolution of *Sardininius* appears to have paralleled that of the myctophiforms in that some basic myctophiform characters occur together with some more advanced characters while several 'premyctophiform' features are still retained, the overall impression being not unlike the Myctophidae.

An additional genus appended here is *Volcichthys*, with the type and only species *Volcichthys dainellii* d'Erasmo (1946), from the Lower Cenomanian of Volci in Comen. This genus was placed by d'Erasmo (1946) in the Enchodontidae, but it most certainly has no affinity with these. From a consideration of Text-figure 98, it can be seen to have a certain degree of similarity with *Sardininius*. Both genera have a long narrow dermal upper jaw, and supramaxillae are absent, but *Volcichthys* has the maxilla entering the gape and bearing teeth. Possibly the two might be related and thus *Volcichthys* can be considered to have a similar origin to that already proposed for *Sardininius*.

The basal stock of the myctophiforms, as represented by *Sardiniooides*, was present at the beginning of the Upper Cretaceous and it has been shown earlier (p. 203, table 1) that great similarities exist between this stock and the ctenothrissiforms. Patterson (1967a) has shown that the ctenothrissiforms gave rise to the beryciforms in the Albian or thereabouts. Thus at the opening of the Upper Cretaceous both the myctophiforms and the beryciforms were present and increasing, whilst the ctenothrissiforms were rapidly declining. Due to the incompleteness of the fossil record little indication can be gained concerning the time of origin of many of the recent myctophiform groups (Patterson, 1967b). *Aulopus* has already been considered in some detail and is little changed from its Cenomanian ancestors. A second recent

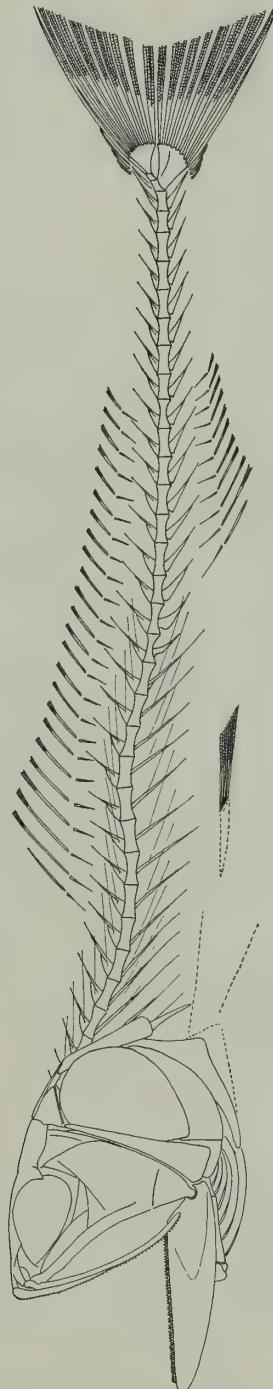


FIG. 98. *Volcichthys dainelli* d'Erasmo. Restoration of the skeleton, scales omitted.

genus, *Chlorophthalmus*, although somewhat more advanced than *Aulopus* is still little different from *Sardiniooides*. The remainder of the recent forms are much more specialized, particularly for life in deeper waters. Harry (1953 : 244) has identified paralepidids in the Miocene of California. These are somewhat more advanced than *Chlorophthalmus*, and are on the line which culminates in the present day *Anopterus* and *Lestidium*. Arambourg (1925) has described a Miocene myctophoid fauna from Licata in Sicily, and his specimens are closely related to the present day Myctophidae. The Californian Miocene deposits certainly seem to be deep water (Crane, 1966 : 20), as do the Sicilian ones.

The colonization of a deep sea environment has been considered by Marshall (1963 : 189) who stated that radiation into the central water masses would have been from a relatively rich to a poor food producing area. The cause of this migration into deeper water can be accounted for if the factor of competition is considered. During the Upper Cretaceous the beryciforms and subsequently the perciforms were radiating and occupying many niches already occupied by salmoniforms and myctophiforms. The acanthopterygians with their more versatile jaw structure, their increased manouevrability and the development of protective mechanisms as well as offensive mechanisms on both fins and scales seem to have provided overwhelming competition for many groups. The Myctophiformes, however, seem to have had sufficient evolutionary plasticity to become adapted to a new environment, that of deeper water. Thus the myctophiforms were able to develop phosphorescent organs, increase the size of the gape, lose the air bladder and decrease the amount of ossification and squamation. Together with these particular specializations the myctophiforms show other trends which are present in the fossil salmoniforms, e.g. enchodontoids and halecoids, and which mirror features seen throughout the Acanthopterygii. These include the loss of the orbitosphenoid, basisphenoid, antorbital and supraorbital; the separation of the parietals; the loss of supramaxillae, and finally the loss of the roof to the post-temporal fossa. In the myctophiforms this reduction is obviously useful in that it reduces the density of the body, but this effect would appear to be only a secondary one. Throughout the Protacanthopterygii and Acanthopterygii, irrespective of habitat and mode of life, the more advanced and specialized members undergo these reductions.

In a discussion of the Myctophiformes some consideration must be given to the Paracanthopterygii of Greenwood, *et al.* (1966). This group represents a parallel spiny-finned radiation to the Acanthopterygii and contains the percopsiforms, batrachoidids, lophioids, ceratioids and gadoids. Greenwood, *et al.* (1966 : 371) proposed that this group might have been derived from some Cretaceous myctophiform such as *Sardiniooides*. They tentatively proposed that a 'paraberycoid' radiation might have occurred, this hypothetical radiation being distinct from the berycoids and the two being independently derived from the Salmoniformes. It is quite possible that the paracanthopterygians represent forms which arose from the myctophiform lineage at about the time that the beryciforms arose. Some degree of substantiation for the alignment of the paracanthopterygians with the myctophiforms is the presence of an adipose fin in both groups. The adipose fin is not

represented in the ctenothrissiforms or the beryciforms. A list of certain basic differences between the two lineages is given below :

Myctophiformes Paracanthopterygii	Ctenothrissiformes Beryciformes
1. Very long alveolar process of the premaxilla under the maxilla.	Alveolar arm much shorter
2. No teeth on the maxilla.	Teeth on maxilla in ctenothrissids and certain berycoids.
3. Supramaxillae small or absent.	Supramaxillae always present and large.
4. No subocular shelf on infraorbital bones.	Subocular shelf present on infraorbital bones.
5. Adipose fin present in myctophiforms and Percopsidae.	Adipose fin never present.
6. Undeepened body.	Body much deepened in the beryciforms.

Together with these differences, Greenwood, *et al.* (1966, p. 388) have pointed out several differences concerned with the levator maxillae muscles and the recurrent facial nerve.

The condition of the caudal skeleton in the paracanthopterygians is unusual (Gosline, 1961, 1963; Rosen, 1962). Instead of the normal fusion of the ural vertebrae with the first preural vertebra followed by subsequent fusion of the upper hypurals to this compound centrum, as has occurred in most higher teleosts, the paracanthopterygians have the upper hypurals fused to the second ural vertebra and this vertebra retains its intervertebral articulation with the fused first preural and ural vertebrae. This condition is approached by certain of the advanced myctophiforms such as *Neoscopelus*, but by none of the beryciforms. *Sardiniodoides* is also similar and additionally has a gap between the second and third hypurals, a feature noticed in many paracanthopterygians. Among other fossil forms *Volcichthys*, noticed earlier (p. 226, Text-fig. 98), has a caudal skeleton closely approaching that of certain amblyopsids. The second ural vertebra has fused with the upper hypurals, while the fused preural and ural vertebrae support the fused first two hypurals as well as the parhypural. A prominent gap is also present between the second and third hypurals. Possibly *Volcichthys* and the related *Sardinius* are close to the 'paraberycoid' hypothetical assemblage, additional support being added by the presence of well developed ctenoid scales in *Sardinius*.

Order CTENOTHRISSIFORMES

The new genus *Pattersonichthys* has been erected to contain several small specimens from the Middle Cenomanian of Hajula, Lebanon. The genus clearly belongs in the order Ctenothrissiformes showing those characters enumerated by Patterson (1964 : 244) for the order. The primitive features visible in *Pattersonichthys* are as follows:

1. Antorbital present.
2. Orbitosphenoid present.
3. Premaxilla small, but with a developing ascending process.

4. Large maxilla supporting two large supramaxillae.
5. Incompletely fused vertebral elements.
6. Numerous epineurals.
7. Parietals meet in the mid-line of the skull-roof.
8. Roofed post-temporal fossa.
9. 17 branched caudal fin rays.
10. No true fin spines. (The anteriormost dorsal fin rays are, however, unsegmented and spinous.) Woodward (1901) initially indicated that *Pateroperca libanica* had three slender spines at the anterior end of the dorsal fin. Patterson (1964 : 371) was of the opinion that these rays were segmented distally and not spinous. In *Pattersonichthys* the first two dorsal rays although composed of ray halves basally show no evidence of having been segmented.

When compared with the genus *Ctenothrissa*, the genus *Pattersonichthys* shows several characters which appear to be more primitive :

1. Parietals meet for their entire length along the mid-dorsal line, and the supraoccipital is small.
2. Post-temporal fossa roofed.
3. Head bones unornamented.
4. Short ascending process on the premaxilla.
5. Maxillary head simple in form.
6. Ceratohyal only slightly deepened.
7. Pelvics sub-thoracic.
8. Scales mainly cycloid.
9. Body undeepened.

Thus the genus *Pattersonichthys* is more generalized than *Ctenothrissa* and lies closer to *Aulolepis* and *Pateroperca*. *Aulolepis*, *Pateroperca* and *Pattersonichthys* are all nearer to the direct ancestry of the Acanthopterygii (*sensu* Greenwood, *et al.*, 1966) than is *Ctenothrissa* itself (see Patterson, 1964). The Ctenothrissiformes as a group present a generalized picture with few specializations (except in *Ctenothrissa*). These more generalized ctenothrissiforms can clearly be derived from the basal salmoniform stock, *Pattersonichthys* differing from this stock in a few details. These include the absence of a supraorbital ; reduction in the number of branchiostegal rays (9) ; reduction in vertebral number ; pelvics sub-thoracic ; mesocoracoid arch absent ; and only one free ural vertebra. These points have already been listed in Table I during the consideration of the Myctophiformes.

The first three of these points are relatively minor changes, whereas the latter three features represent more fundamental changes in organization, correlated with a greater efficiency in movement. The loss of the mesocoracoid arch is due to the migration up the flank of the pectoral fin, from which position the pectoral fin may act as a brake. The forward migration of the pelvic fins is correlated with the use of the pectorals as brakes, the pelvics being used as stabilizers (Harris, 1938 : 37 ; Patterson, 1964 : 452). The consolidation of the caudal skeleton is the first of

many steps to reduce the number of moveable parts in the caudal fin. The tail is only required to move in one plane and it would seem that fusion of component parts would produce a more effective fin. In the most advanced perciforms the consolidation has reached an end point in which the caudal skeleton is only formed from one or two large plates.

An historical review of the Ctenothrissiformes has been given by Patterson (1964 : 241). In this work Patterson considered three genera, *Ctenothrissa*, *Aulolepis* and *Pateroperca*, which he put into two families :

Family Ctenothrissidae. *Ctenothrissa*.

Family Aulolepididae. *Aulolepis* and *Pateroperca*.

In his discussion (Patterson, 1964) of the affinities of *Ctenothrissa* he concluded that " *Ctenothrissa* is a form which has evolved towards the acanthopterygians in a number of characters (thoracic pelvics, no mesocoracoid, ctenoid scales, and deep body in particular), while still showing unmistakeable signs of an elopoid ancestry (small supraoccipital, foramen for orbital artery, antorbital, toothed maxilla, and incompletely fused vertebral elements), yet has become specialized in ways which exclude it from the direct ancestry of the acanthopterygians ". However, *Aulolepis* shows several differences to *Ctenothrissa*, but as Patterson (1964) points out, these are only in degree. *Pattersonichthys*, like *Aulolepis* and *Pateroperca*, is more generalized than *Ctenothrissa* and is included in the family Aulolepididae.

One salient feature of *Pattersonichthys* not found in any other ctenothrissiform genus is the roofed post-temporal fossa. The absence of a roofed fossa excludes both *Aulolepis* and *Pateroperca* from the direct ancestry of the Beryciformes, since a partially roofed post-temporal fossa is still present in the early beryciforms (*Hoplopteryx*, *Trachichthyoides*, Patterson, 1964 ; *Lissoberyx*, *Caproberyx*, Patterson, 1967a). The presence of a roofed fossa in *Pattersonichthys* suggests that it is nearer to the direct line of ancestry of the Beryciformes than is either *Ctenothrissa*, *Aulolepis* or *Pateroperca*.

Patterson (1967a : 106) has suggested that the ancestral beryciform stock would have possessed the following characteristics :

1. Of small size with unornamented head bones.
2. High supraoccipital crest from a moderately large supratemporal fossa.
3. Reduced antorbital.
4. Toothed maxilla.
5. Scaly operculum.
6. Partial roof to the post-temporal fossa.

These characters are all present in the Ctenothrissiformes but in mosaic occurrence *Pattersonichthys* for example shows 1, 3, 4 and 6 but not 2 and 5.

The basic caudal pattern shown by the Ctenothrissiformes (Text-fig. 77) and Beryciformes (Patterson, 1968b) is similar to that already seen in the Myctophiformes (Text-fig. 72). This type of caudal skeleton was also present in several of the fossil salmoniform groups mentioned in this work, the Enchodontoidei (Text-fig. 42), Halecoidei (Text-fig. 64) and Cimolichthyoidei.

All of the groups mentioned above except the Beryciformes are included within the Protacanthopterygii (*sensu* Greenwood, *et al.*, 1966), whose basal stock is represented by the salmonoids. From a caudal skeleton like that of *Salmo* (Text-fig. 81) all of these other groups can be derived by the fusion of preural vertebra one with ural vertebra one. The basic caudal composition of the Enchodontoidei, Cimolichthyoidei, Halecoidei, Myctophiformes, Ctenothrissiformes and Beryciformes is as follows :

1. Preural vertebra one fused with ural vertebra one.
2. Ural two present as a terminal half-centrum.
3. Six hypurals.
4. Three epurals.
5. A stegural formed from uroneural one and neural arch components.
6. A second uroneural behind the stegural.

A variable feature in the caudal skeleton of these six groups is concerned with the neural arch and spine of the second preural vertebra (i.e. the first free preural vertebra). In the Beryciformes, Patterson (1968b) states that the polymixoids and some dinopterygoids retain the neural spine of preural vertebra two while in the remaining dinopterygoids and the berycoids the spine is lost. In the Ctenothrissiformes, *Ctenothrissa*, *Aulolepis* and *Pattersonichthys* have lost the neural spine, and it is only retained in *Pateroperca*.

Thus in respect of the post-temporal fossa *Pattersonichthys* is closest to the ancestry of the beryciforms, but in caudal structure is further removed than *Pateroperca*. Patterson's (1964) conclusions are still valid in that no so far described ctenothrissiform could have been directly ancestral to the beryciforms, although this ancestry clearly lies within the ctenothrissiform grade.

Patterson (1964 : 465) has also used the distribution in time of the ctenothrissiforms as supporting evidence that the group is near the ancestry of the Acanthopterygii as a whole. The more generalized members of the Ctenothrissiformes, which are rare in the Cenomanian, have died out by the Turonian, being replaced by the more specialized beryciforms which they had given rise to in the Albian or earlier (Patterson, 1967a : 107). The more specialized *Ctenothrissa*, which parallels the beryciforms to a certain extent, seemed able to compete with the berycoids and continued into the Turonian. This distribution is to be expected if the more generalized ctenothrissiform stock (represented by *Aulolepis*, *Pateroperca* and *Pattersonichthys*) had given rise to the Beryciformes.

Patterson (1964) has evaluated the merits of deriving the Acanthopterygii from the Ctenothrissiformes or from the Myctophiformes, and has shown conclusively that the ancestral stock lies closer to the ctenothrissiforms. He further indicated that the Ctenothrissiformes were not closely related to the generalized Myctophiformes although both groups had reached the same stage of evolution. As has already been indicated in the discussion of the myctophiforms both of these groups are far more closely related than Patterson (1964) supposed. Furthermore it has also been indicated that the bases of both groups are little removed from a basal salmoniform

stock. For example *Pattersonichthys delicatus* differs from *Sardiniooides minimus* in the following features :

1. A small broad ascending process with a short alveolar arm on the premaxilla.
2. Long, stout maxilla which is extensively toothed, forming two-thirds of the gape.
3. Two very large supramaxillae.
4. Unexpanded suboperculum.
5. Sub-thoracic pelvic fins.
6. Cycloid scales which do not extend on to any of the skull bones.
7. Fulcral scales reduced in extent.

Apart from these points the two genera are practically identical in all respects. Thus two groups (Ctenothrissiformes and Myctophiformes) which are ordinally separated have basal members which converge strongly, although the ctenothrissiform and myctophiform lineages are evident in the convergent stocks. Patterson (1967a : 104) has considered a similar basal convergence of the trachichthyid and holocentrid berycoids at the base of the Cenomanian.

Although it has now been indicated that the basal myctophiforms and ctenothrissiforms are on equivalent levels of structural organization, the evolutionary potential within either group would appear to be different. The ctenothrissiforms were endowed with the ability to produce a higher level of organization, the Acanthopterygii (*sensu* Greenwood, *et al.*, 1966). The evolutionary potential in the myctophiform lineage would appear to have been limited solely to producing diversified members of the same structural level of organization, although certain of the descendants are extremely specialized for particular habitats. This viewpoint, however, excludes the possibility of the basal myctophiforms having given rise to the Paracanthopterygii (the parallel spiny-finned radiation) as Greenwood, *et. al.*, (1966) supposed. If the myctophiforms did give rise to the Paracanthopterygii then the evolutionary potential of the myctophiforms and ctenothrissiforms was similar.

IV. TELEOST EVOLUTION WITHIN THE CRETACEOUS

Before the evolution of the teleosts in the Cretaceous can be considered it is necessary to give some discussion of the evolution of the teleosts as a whole. The first question to be answered is whether or not the teleosts represent a monophyletic group or a polyphyletic one. Patterson (1967c : 95) has given this question some thought but indicates that one must first settle upon the definition to be attached to the term polyphyletic. Recently most authors have considered that the teleosts had their origin within the halecostomes. Thus monophyly occurs at the level of the division Halecostomi. If, however, within the halecostomes it is found that more than one family had given rise to the teleosts, then polyphyly is present at the familial level. This point is discussed in some detail by Patterson (1967c), who is of the opinion that no grounds have so far been put forward which detract

from the idea that the teleosts are monophyletic at the level of the family Pholidophoridae.

The division Halecostomi represents a transition grade between the basal holosteans and the teleosts and was first used by Woodward (1932). The central stock of the halecostomes would appear to be the family Pholidophoridae, and Gardiner (1960) has convincingly shown that this family can be derived directly from the early Parasemionotiformes. The family Pholidophoridae is normally grouped with five other families in the order Pholidophoriformes (see Griffith and Patterson, 1963, for consideration of these families). The Pholidophoridae appears to be closest in structural organization to the teleosts whereas the other families are more distantly removed.

The Pholidophoridae *sensu stricto* have recently been extensively examined by Nybelin (1966) who agrees with Gardiner (1960) that they were derived from a parasemionotid-like ancestor. In confirmation Griffith and Patterson (1963 : 37) stated that the parasemionotids are almost ideal intermediates between the chondrostleans and the halecostomes.

The division Halecostomi also includes the order Leptolepiformes, and this order, together with the Pholidophoriformes, presents a collection of families which exhibit a mosaic of halecostome and teleostean characters (mosaic evolution is used in the sense that de Beer, 1954, and Schaeffer, 1965, indicated, viz. lineages of common ancestry exhibiting various combinations of primitive, intermediate and advanced characters). Schaeffer (1965 : 322), in reference to the origin of the teleosts, indicated that every organism is a mosaic whether or not it is associated with a transition between grades or with an adaptive radiation within a grade. The latter point has been amply illustrated in the foregoing discussions where radiations within the Salmoniformes have been considered. It is hoped that the former point will become apparent throughout this section.

This mosaic nature of the halecostomes makes it difficult to define a 'teleost'. Patterson (1967c) has argued the 'pros and cons' of the dilemma and whether or not it is advisable to recognize the Teleostei as a taxonomic group. Lehman (1966) and Berg (1940) for example do not recognize a division Teleostei, but Patterson (1967c : 95) finds that a category Teleostei is necessary and that the base of this group is within the leptolepids.

The teleost characters shown by the halecostomes are related to changes in respiratory, feeding and locomotor mechanisms and include :

1. Loss of enameloid tissue (ganoine) from scales and dermal bones.
2. Thinning of scales and loss of the peg and socket joint.
3. Ossification of the vertebrae as single units.
4. Development of numerous intermuscular bones.
5. Compact caudal skeleton with two hypurals to the lower caudal lobe supported on ural vertebra one.

These features all indicate the increased flexibility of the body and compensate in part for the increased mechanical stresses built up by the musculature (Nursall, 1956). One primitive character of the halecostomes is the presence of enamel as a thin layer

covering the scales and dermal bones in pholidophorids (Nybelin, 1966). The loss of enamel has made possible the sinking inwards of dermal bones of the skull and the production of uroneurals in the caudal fin skeleton in teleosts. This latter feature, concerning the internal uroneurals attached to the ural vertebrae, has been used by Patterson (1967c) provisionally as a diagnostic feature of teleosts.

The leptolepids have convincingly been shown to have their origin within the Pholidophoridae (Rayner, 1948 : 338), and several authors (Rayner, 1948 : 340 ; Griffith and Patterson, 1963 : 40) have proposed that the Leptolepididae gave rise to the remainder of the teleosts. Other authors have supposed only the clupeoids to be direct derivatives of the leptolepids. Gardiner (1960 : 351) has indicated that both the Clupeidae and Chirocentridae can be derived from the leptolepids, all three groups having no bone cells in their scales, whereas elopoids and salmonoids, which still retain bone cells in the scales, must have evolved from pholidophorids. Greenwood, *et al.* (1966) have stressed that the Clupeomorpha have several unique characters which have so far not been elucidated in the leptolepids. Patterson (1967c) has considered the origin of the Clupeomorpha in detail and has refuted Bardack's (1965) hypothesis concerning the derivation of the Chirocentridae from forms like the ichthyodectids and the Upper Jurassic *Thrissops* and *Allothriissops*. The origin of the Clupeidae according to Saint-Seine (1949) from a form like *Leptolepis coryphaenoides* has also been refuted by Patterson (1967c). Woodward (1942b : 908) postulated the derivation of *Diplomystus* from a pholidophoroid and not from a leptolepid because of the presence of ridge scutes behind the pelvics in the diplomystids and in some pholidophorids. This character of Woodward's (1942b) is insignificant, but nevertheless his idea of deriving the clupeoids from a pholidophorid and not a leptolepid is sound. Arambourg (1954), in describing the new genus *Clupavus*, related it to the clupeoids, in particular the Dussumieriidae. Patterson (1967c) has convincingly shown this to be incorrect and has demonstrated the closeness of *Clupavus* to the leptolepids, and their dissociation from the clupeomorphs. Greenwood, *et al.* (1966 : 360) are in agreement with Patterson (1967c), and both propose a connection between *Clupavus* and *Leptolepis* in a convergent evolutionary trend to the Clupeomorpha. This provides an instance of what Schaeffer (1965 : 322) maintained when he stated, "mosaics which in retrospect are involved in a transition to a higher level, may be modified in much the same way in a number of related lineages".

The Elopiformes represent the most primitive of living teleosts and this group retains the greatest number of halecostome characters. Gardiner (1960 : 351) has indicated that on scale structure alone the Elopiformes could be derived most satisfactorily from a pholidophoroid but not from a leptolepid. Saint-Seine (1949) has described a late Jurassic 'protelopid' *Eoprotelops*, but Gardiner (1967b) considers this to be a halecostome, and Patterson (1967b) also indicates that it is not an elopoid. Bertin and Arambourg (1958 : 220) had previously appended *Eoprotelops* to the family Leptolepididae.

An elopid caudal skeleton has been described from the late Jurassic by Nybelin (1963) and it is probable that the elopiform lineage was in existence throughout

the early Jurassic, competing with the leptolepids and pholidophorids, as well as the majority of the Holostei. The elopids and the leptolepids thus appear to represent independent attainments of the teleost level, if the leptolepids are considered to be teleosts.

The similarities between the Pholidophoridae, Elopidae and Leptolepidae can conveniently be listed :

1. No articular or ascending processes on the premaxilla.
2. Rostral elements with a bone enclosed ethmoidal commissure.
3. Several supraorbitals.
4. Fringing fulcral scales.
5. Gular plate present.
6. Many posterior branches from the preopercular sensory canal.
7. No stegural.
8. No adipose fin.

The Salmoniformes represent a further teleost stock which shows a wide divergence from the Elopiformes. This divergence has been indicated by Greenwood, *et al.* (1966) who have given superordinal rank to these two phyletic lineages. The basal salmoniform stock exhibits many differences not only from the elopiforms, but from the pholidophorids and the leptolepids. These differences include :

1. Articular process on the premaxilla.
2. No separate dermal rostrals, no bone enclosed commissure.
3. One small supraorbital.
4. No fringing fulcra.
5. No gular plate.
6. No posterior branches of preopercular sensory canal.
7. Stegural present.
8. Adipose fin present.

Several further dissimilarities are seen between the Recent forms *Megalops* and *Salmo*. *Megalops* has an otophysic connection, a leptocephalus larva, parasphenoid teeth and a subtemporal fossa.

Discussion of the origin of the Salmoniformes is rendered difficult by the complete absence of fossil material below the Albian stage of the Lower Cretaceous. However, any one of these features in which the Salmoniformes differ from the Pholidophoridae could have been derived directly by reduction or loss through intermediate forms, as yet unknown, presumably within the Jurassic. For example, Nybelin (1967 : 244) has shown that the bone enclosed ethmoidal commissure of the elopoids is homologous with the canal system embedded in the soft tissue of the snout of clupeoids, and the pit-line on the snout of salmonoids. The commissure, then, in the salmonoids, has lost its bony surround together with any other rostral elements, except for the antorbital. Gardiner (1960 : 351) has said that the Salmonidae and Characiniidae can be derived much more easily from a pholidophorid ancestor than from a leptolepid one, not just on scale structure, but on general disposition, in particular of the jaws. From my own observations I think it impossible to derive a basal salmoniform from a leptolepid such as *Leptolepis africana* Gardiner (1960 : 314, fig. 48)

because of the enormous coronoid process of the mandible of *Leptolepis*, and the practically edentulous condition of the jaws as a whole. Other leptolepids however, e.g. *Leptolepis coryphaenoides* (Bronn) (Text-fig. 99D) and *Leptolepis normandica* Nybelin (Text-fig. 99C) have a lower coronoid and are provided with rather more teeth. The Pholidophoridae also exhibit a relatively large coronoid and small teeth (except *Pholidophorus similis*, Saint-Seine 1949, although Saint-Seine's reconstruction of this fish is to be viewed with some reservation). This does not imply that the salmoniforms were not derived from some pholidophorid, as the jaws are a particularly labile entity capable of easy modification. Thus it is conceivable that a leptolepid such as *Leptolepis normandica* may have provided the ancestral salmoniform stock.

Possibly a trivial character, but one worth mentioning, is the suprapreopercular bone bearing the upper part of the preopercular sensory canal (formed from the fragmentation of the upper part of the preoperculum). This bone is seen in the salmonid *Salvelinus* (Norden, 1961), certain Gonorynchiformes and many Ostariophysii (Greenwood, *et al.*, 1966). Greenwood, *et al.* (1966) have indicated the extreme primitiveness of these three groups and place them near to the base of the protacanthopterygian radiation. Greenwood, *et al.* (1966 : 382) describe the ostariophysan suprapreoperculum as "an ossicle above the uppermost part of the preoperculum and partially surrounding the sensory canal". It seems probable that since it is a canal bearing bone, the suprapreoperculum would have been present in the ancestral form. Fragmentation of the preoperculum occurs throughout the Chondrostei, including the Parasemionotidae (see Gardiner, 1967a : 200). In most cases it is the non-canal bearing anterior part of the preoperculum which fragments to produce the suborbital series. Less frequently the canal bearing portion of the preoperculum also fragments to give a smaller suprapreoperculum dorsally (Gardiner, 1967a, fig. 2A). Such a condition is seen in *Parasemionotus laborei* Piveteau (Text-fig. 99A) and the totally unrelated chondrostean *Boreosomus gilliotti* Priem. No so far described pholidophorid has a suprapreoperculum (see Nybelin, 1966). However, Nybelin (1962) has shown in both *Leptolepis coryphaenoides* and *Leptolepis normandica* a large suborbital, and has indicated that beneath the suborbital of the latter there is a separate suprapreoperculum. If this in fact is such a variable feature then no importance can be attached to it. But if both suborbital and suprapreoperculum are formed from the fragmentation of the preoperculum, as Gardiner (1967a : 199) has shown, it is hard to believe that one fragment could completely cover the other, especially as the covered fragment is canal bearing. Nevertheless it has already been seen that on scale structure the leptolepids are off the ancestry of the salmoniforms (Gardiner, 1960). A suprapreoperculum is not known in any other halecostome. It would seem unlikely that further fragmentation of the preoperculum within the halecostomes or early teleosts would have taken place since by the halecostome grade of organization the preoperculum had become more and more intimately associated with both the jaw musculature and the underlying palate (Gardiner, 1967a).

Thus it may be that some as yet unknown pholidophorid which retained the parasemionotid suprapreoperculum gave rise to the salmoniforms, gonorynchi-

forms and ostariophysans (the basal forms within the Protacanthopterygii). A possible reason for the absence of this ancestral stock and for the apparent absence of Salmoniformes before the Lower Cretaceous, and of Ostariophysi before the

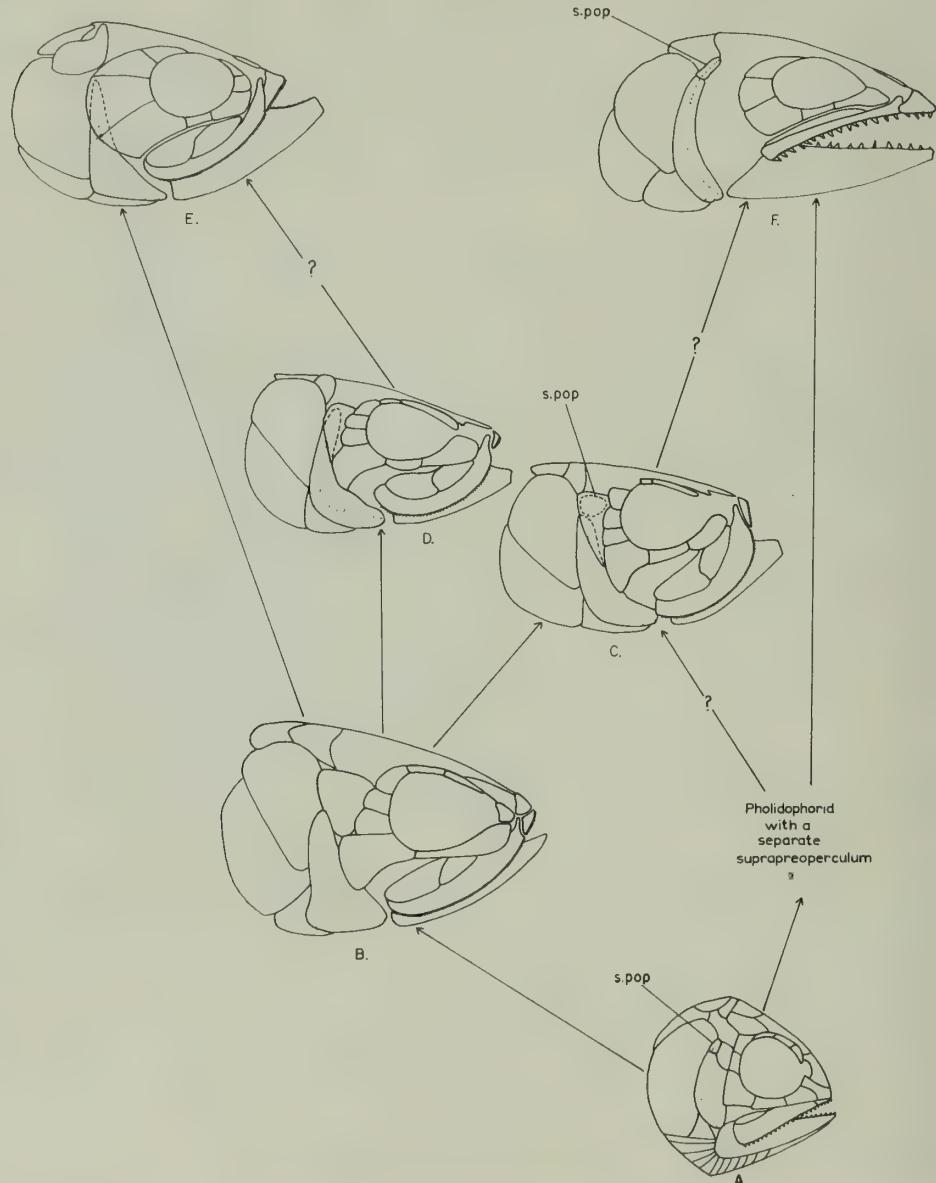


FIG. 99. Outline restorations of certain halecostome and teleost skulls to indicate possible relationships. (A) *Parasemionotus labordei*. After Gardiner (1960). (B) *Pholidophorus bechei*. After Nybelin (1966). (C) *Leptolepis normandica*. After Nybelin (1962). (D) *Leptolepis coryphaenoides*. After Nybelin (1962). (E) *Megalops cyprinoides*. (F) *Salvelinus* sp.

Tertiary, is that the early evolution of these groups could have occurred in fresh-water, and fresh-water deposits are rare. This proposition has already been tentatively suggested by Greenwood, *et al.* (1966 : 347). The Ostariophysi and Gonorynchiformes are predominantly fresh-water forms, while many of the present day Salmonoidei spend the breeding part of their lives in fresh-waters. Possibly then the ancestral stock of the Protacanthopterygii as a whole was to be found in fresh-water. This hypothesis would also help to explain the divergence between the Elopiformes and the Leptolepididae on the one hand and the Salmoniformes on the other, the initial evolution of the two groups occurring in marine and fresh waters respectively.

No mention in the discussion so far has been given of the Osteoglossomorpha of Greenwood, *et al.* (1966). This division they tentatively considered to have a separate origin in the Pholidophoridae. Patterson (1967c : 107) indicates that they could have been derived with the Ichthyodectidae from such Jurassic forms as *Allothrissops*. Bardack (1965), however, postulated the derivation of the Chirocentridae from forms such as *Thrissops* and *Allothrissops*. Both Cavender (1966) and Patterson (1967c) refute this, the latter suggesting that these two genera are convergent with the clupeoids and were derived from a leptolepid and not a pholidophorid as Bardack (1965) suggested. Patterson (1967c) thus thinks that the Osteoglossomorpha can be placed with the Elopomorpha, Clupeomorpha and the Leptolepididae as a related group of lineages. The osteoglossomorphs however are predominantly fresh-water and may have arisen in this medium with some closer affinity with the basal protacanthopterygians.

There is apparently a 'time-lag' between the origin of the teleosts as a whole and their explosive radiation in the Cretaceous. Both the Pholidophoridae and Leptolepididae occur in the Triassic and the elopiforms are represented in the Jurassic. This lag in the radiation of the teleosts during the Jurassic occurred at the time of the maximum holosteian diversification. Schaeffer (1965) has pointed out that the ecological situation at this time is difficult to assess, so that the role that competition might have played is impossible to determine. It is possible, as Schaeffer (1965) indicated, that the superior halecostome locomotor mechanism plus the plastic pholidophoroid jaw design was gradually perfected throughout this period and the teleost grade began to exhibit its tremendous potential at the end of the Jurassic. It would appear that the elopoids and leptolepids (which arose in the Triassic and Lower Jurassic) did not represent a significant advance over the Holosteoi and merely existed as contemporaries. However if the halecostome ancestors of the salmoniforms had moved into fresh-water in the late Triassic and Jurassic, and gradually evolved during that period in the absence of competition from the holosteans, then this time-lag would not be so apparent. Finally at the close of the Jurassic sufficient evolutionary advance had been accomplished by the protacanthopterygians to provide overwhelming competition for the holosteans and the group re-entered the seas. Once back in a marine environment in the Cretaceous, the Protacanthopterygii rapidly diversified giving the appearance of an 'explosive radiation' at the sub-ordinal and familial levels.

It now remains to consider the evolution of the teleosts within the Cretaceous period. The order Elopiformes is represented in the Cenomanian by *Sedenhorstia* which differs little from the Recent *Elops* and *Megalops* (Goody, 1969). Already Nybelin (1963) has indicated the presence of an elopiform in the Jurassic, thus the elopoid assemblage is an ancient one and would appear to have changed little from the Jurassic to the present day. Greenwood, *et al.* (1966 : 355) have indicated that the albuloids were established by at least Eocene times and probably earlier since they recognize that the Upper Cretaceous *Istieus* shows strong affinities with *Pterothrissus*. The two further derivatives of the basal elopomorphs are the eels and the notacanths. Both of these groups are represented in the upper Cretaceous ; eels by *Urenchelys* Woodward (1901) and *Anguillavus* Hay (1903) ; notacanths by the halosaur relatives *Echidnocephalus* von der Marck (1863) and *Enchelurus* Woodward (1901). These forms are little different from the modern representatives and their origin must have been at least in the Lower Cretaceous or even in the Jurassic.

The basal stock of the Protacanthopterygii probably radiated into marine environments at the end of the Jurassic and the beginning of the Cretaceous and is represented by the Salmoniformes. Greenwood, *et al.* (1966) have erected several suborders within this order, each representing a small radiation from the basal stock ; the Esocoidei, Stomiatoidei, Argentinoidei and Galaxioidei represent certain of these radiations. The suborder most closely approaching the basal stock is the Salmonoidei. In the foregoing systematic account four further suborders have been added to the Salmoniformes, the Ichthyotringoidei, Cimolichthyoidei, Enchodontoidei and Halecoidei, each representing a small radiation of related forms readily separable from each other. These fossil suborders represent equivalent groupings to the seven or eight salmoniform suborders listed by Greenwood, *et al.* (1966 : 394).

The Ichthyotringoidei represents the earliest offshoot from the salmoniform stock and is represented in the Gault by *Apateodus*. This genus existed practically unchanged throughout the Upper Cretaceous and finally disappeared in the Maastrichtian. The two families within the suborder, the Ichthyotringidae and the Apateopholidae, are both derivable from an *Apateodus*-like ancestral form by extension of the snout (Text-fig. 100).

The Cimolichthyoidei has been divided into two groups, the cimolichthiid/dercetid group and the prionolepid group. If they are related then the dichotomy between the two must have occurred soon after the derivation of the group as a whole from the ancestral stock. The Prionolepididae continued into the Turonian without diversification. The Dercetidae on the other hand had their origin within the Cimolichthiidae but radiated quite considerably. For example the very specialized long-snouted, long-bodied dercetid *Rhynchodercetis* extends from the Lower Cenomanian to the Middle Cenomanian and must have arisen in the Lower Cretaceous (Albian ?). *Pelargorhynchus*, although not appearing in the fossil record until the Upper Senonian, must have originated from a basal dercetid stock which still retained a complete squamation. Since all of the known Upper Cretaceous dercetids have a reduced squamation the origin of *Pelargorhynchus* was presumably well down into the Lower Cretaceous, before the origin of the *Rhynchodercetis* line. *Dercetis*

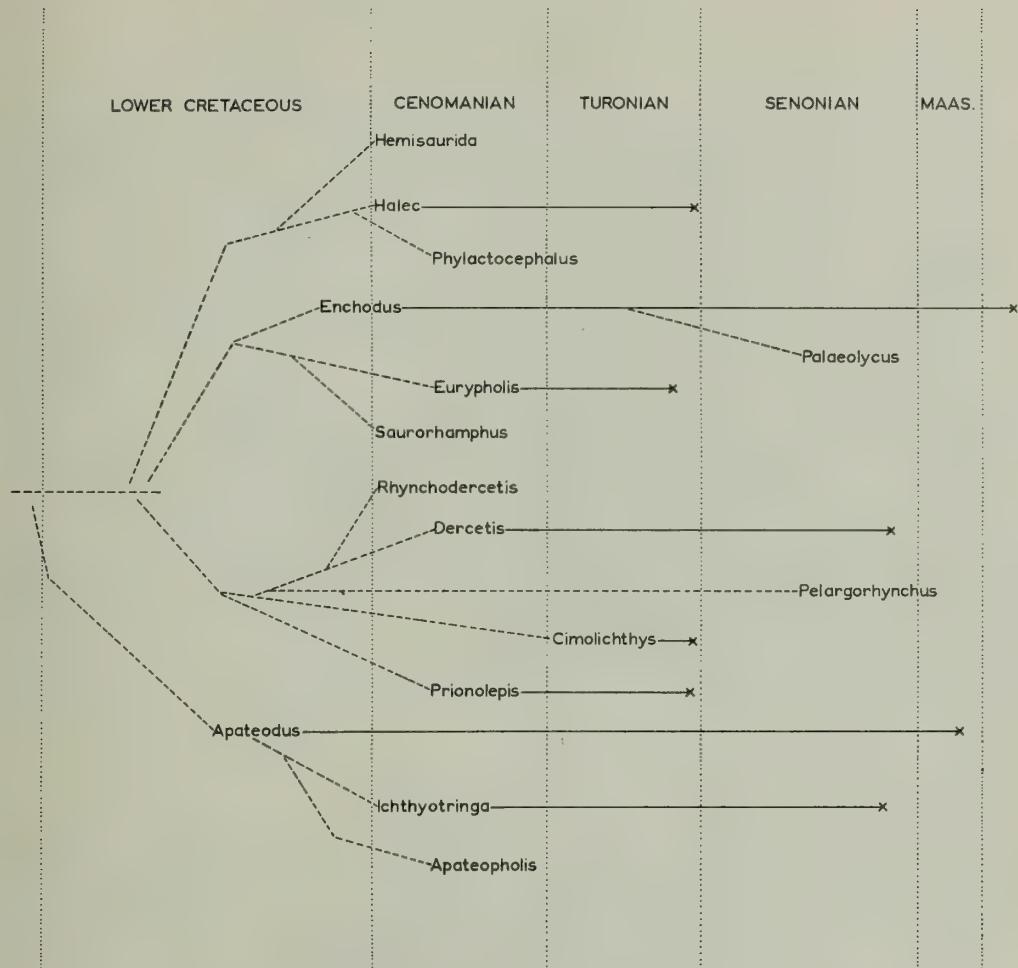


FIG. 100. Evolutionary tree of the fossil salmoniform suborders.

itself extends through the Upper Cretaceous and disappears at the end of the Senonian (Text-fig. 100).

The Enchodontoidei is composed of two families, the Enchodontidae and Eurypholidae. The genus *Enchodus* extended throughout the Upper Cretaceous and is recorded from the Tertiary (Arambourg, 1952). The divergence between the two families must have occurred in the Lower Cretaceous since a specialized derivative of the Eurypholidae, *Saurorhamphus*, is present in the lowermost Cenomanian. The genus *Eurypholis* is not recorded until the Middle Cenomanian and extends through into the Turonian. *Saurorhamphus* can be derived directly from *Eurypholis*, merely by slight snout and body extensions. *Palaeolycus* represents a specialized derivative of the Enchodontidae and occurs in the Upper Senonian. The origin of this genus can be visualized as being from one of the shallower bodied species of *Enchodus*, in which vertebral multiplication occurred. This origin was presumably in the Upper

Cretaceous, since there are no factors excluding the genus *Enchodus* from having been the immediate ancestor of *Palaeolycus* (Text-fig. 100).

The Halecoidei are represented in the Lower Cenomanian by the most primitive genus *Halec* (d'Erasmo, 1946). *Phylactocephalus* occurs in the Middle Cenomanian and could easily have been derived directly from *Halec* at the end of the Lower Cretaceous. *Hemisaurida* also had its origins within the same basic stock, but would appear to have branched off at a slightly earlier stage than *Phylactocephalus*, since *Hemisaurida* is already represented in the Lower Cenomanian. The genus *Halec* remained the most generalized form and extended into the Senonian (Text-fig. 100).

In the discussions of these fossil salmoniforms, I have attempted to show that they have evolved along lines represented throughout the division Protacanthopterygii and to a more marked extent parallel the Myctophiformes and the Acanthopterygii. Each of the suborders dealt with earlier appears to express similar evolutionary capabilities. Within the recent Salmoniformes the Galaxioidei (*Galaxias* and *Aplochiton*) are often cited as being practically indistinguishable from the Myctophiformes especially with regard to the upper jaw (Greenwood, *et al.*, 1966 : 366; Gosline, Marshall and Mead, 1966 : 2). Thus a recent suborder reinforces the suggestion of the similarity in evolutionary potential between the fossil salmoniforms and the myctophiforms. It would seem that several of the salmoniform suborders have the potential, latent or expressed, to produce a more advanced structural complex which in most cases approaches the myctophiform grade. Thus the myctophiform grade (although it is proposed in this work that the order Myctophiformes is itself monophyletic) can be attained by other Salmoniformes.

The acanthopterygian complex of characters represents a considerable advance over and above the most advanced Salmoniformes and Myctophiformes. The major advances in feeding, locomotion and protection are exemplified by the protrusile upper jaw, thoracic pelvics, body shortening and deepening, and the development of spines in fins and on scales. These features are only encountered together in the single line stemming from the protacanthopterygian order Ctenothrissiformes (Patterson 1964). (True protrusibility of the jaws never occurs in the Paracanthopterygii, although all of the other features listed above are shown.) The Ctenothrissiformes have been shown to be little removed from a basal salmoniform stock (Table I, p. 203) and also to be very similar to a basal myctophiform (e.g. *Sardinioides*). The common ancestry of these two groups (Ctenothrissiformes and Myctophiformes) occurs in the Lower Cretaceous. The Myctophiformes are well established by the Middle Cenomanian and would appear to have had their origin in the Albian. *Nematonotus* has been mentioned as being a genus which approaches both Myctophiformes and Ctenothrissiformes, substantiating the basal convergence of the two groups. *Nematonotus* occurs in the Cenomanian together with *Acrognathus*, which also approaches both groups. *Sardinius*, however is a probable derivative of the very early myctophiform lineage despite its late appearance in the fossil record (Upper Senonian). *Sardinius* closely parallels the family Myctophidae, particularly in the backwardly inclined suspensorium and the absence of supra-

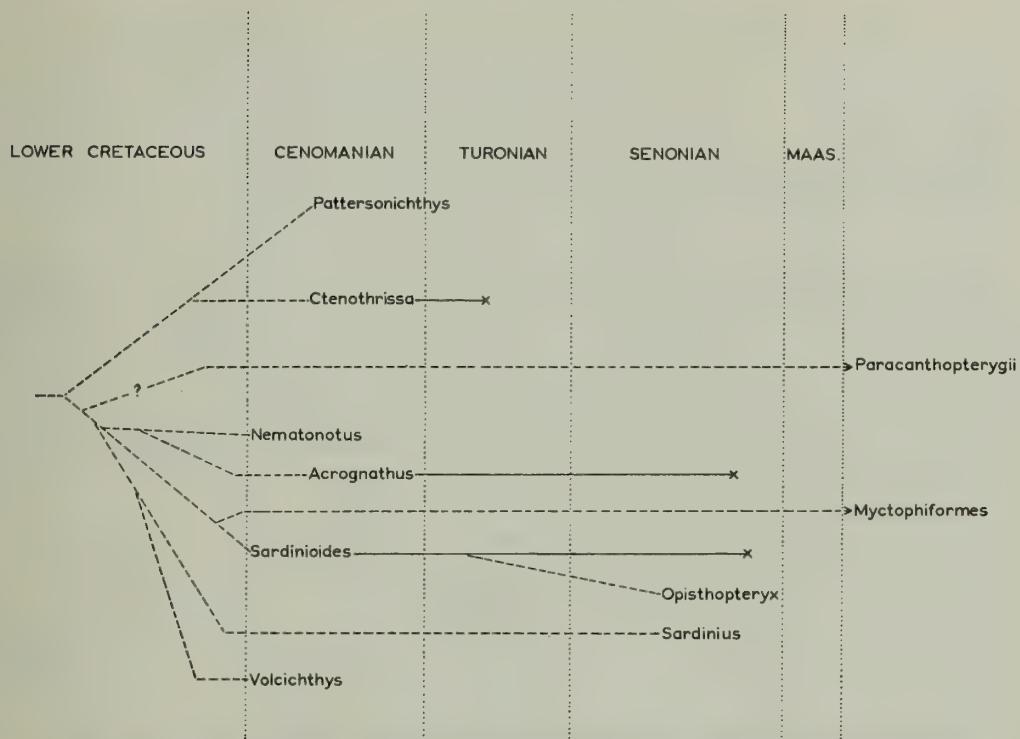


FIG. 101. Evolutionary tree of the Myctophiformes and Ctenothrissiformes within the Cretaceous.

maxillae. *Volcichthys*, from the Lower Cenomanian, is tentatively suggested to be related to *Sardinius*. The Upper Senonian genus *Opisthopteryx* appears to have been derived from a form not unlike *Sardinoides* (Text-fig. 101).

Patterson (1967a) has indicated that the Beryciformes probably arose sometime in the Albian from a ctenothrissiform stock. By the end of the Lower Cretaceous salmoniform derivatives were numerous and had undergone a considerable degree of radiation. Having given rise to the Ctenothrissiformes and the Myctophiformes, the basal stock appears to have continued and produced yet further lineages, none however corresponding to the ctenothrissiforms but some paralleling the myctophiforms. The Stomiatoidei is possibly represented in the Lower Cenomanian by *Paravinciguerria* (Arambourg, 1954). Weitzman (1967 : 535–537) has evaluated the fossil record of the stomiatoids, and has reached the conclusion that *Paravinciguerria* may be stomiatoid, whereas *Idriussia* (Arambourg, 1954) is probably not. The Argentinoidei, Galaxioidei and Esocoidei do not appear in the fossil record until the Tertiary (Patterson, 1967b). The argentinoids and galaxioids presumably arose in the Upper Cretaceous or actually in the Tertiary itself, but the Esocoidei, in view of the structure of their dermal upper jaw, present more of a problem. The separate proethmoid of *Esox* and *Dallia* may be the forerunner of an ascending process or it might be only an analogous structure indicating the derivation of the Esocoidei

from the basal salmoniform stock before forms such as the myctophiforms and ctenothrissiforms had arisen. Weitzman (1967 : 526) doubts that the proethmoids of esocoids have any relation to the evolution of the ascending premaxillary processes in other teleosts. He suggests that the esocoids exhibit an experiment in jaw design which did not impart any significant evolutionary advantages. Due to the fresh-water habitat of the Esocoidei this group may represent an early offshoot from the salmoniform ancestral stock in the Jurassic fresh waters.

The fossil salmoniform suborders Enchodontoidei, Ichthyotringoidei, Cimolichthyoidei and Halecoidei extend throughout the greater part of the Upper Cretaceous, but all seem to have disappeared by the Maastrichtian. The myctophiforms are represented throughout the Upper Cretaceous but the ctenothrissiforms had disappeared by the Middle Turonian, this latter group having been replaced by its more advanced descendants, the Beryciformes. The Beryciformes were evolving and diversifying throughout the Cretaceous, and towards the close of this period several of the lines represented in the present day Beryciformes and Perciformes were established (Patterson, 1964, 1967a, 1967b).

In the Cretaceous period the Elopiformes, Anguilliformes, Notacanthiformes, Clupeiformes, Osteoglossiformes, Salmoniformes, Myctophiformes, Ctenothrissiformes and Beryciformes would have inhabited similar environments and would have been in direct competition with each other for food and living space. The Cretaceous fauna would have lived in the most productive parts of the ocean, these favourable parts being inshore waters (above the upper reaches of the continental shelves) or the surface waters of equatorial oceanic regions (Marshall, 1963 : 189). Throughout the Upper Cretaceous the Beryciformes were increasing and perfecting the protrusile mouth which opened up new and hitherto unused food sources. At the same time the Beryciformes were becoming more effective swimmers and were developing protective spines on fins and scales. A true protrusile mouth is not developed in any other group, although all the basic requirements are present in the Myctophiformes. Towards the close of the Cretaceous the Beryciformes gave rise to lines leading on to the Perciformes and other advanced Acanthopterygii (Patterson, 1964, 1967a). Thus the beryciforms and their derivatives would have provided stern competition for the less labile, more primitive grades of organization represented by the Elopiformes and the early salmoniform derivatives. Many of these lower teleostean groups succumbed to this pressure of competition and died out, e.g. Enchodontoidei, Cimolichthyoidei, etc. Others, better adapted to their particular habits, e.g. Clupeomorpha, or modified along very specialized lines, e.g. eels, were able to survive and compete. Still others at the end of the Cretaceous were forced to seek living space elsewhere. This involved the colonization of the less productive parts of the ocean, which include the central water masses at increasing depths. Thus groups like the myctophiforms and stomiatoids were forced into deeper waters. It is interesting to note that the vast majority of the recent bathypelagic fish are all lower teleostean in origin. Once in the bathypelagic environment a certain amount of adaptive radiation has occurred in both of the above mentioned groups, this radiation commencing at the close of the Cretaceous and the beginning of the Tertiary. Thus

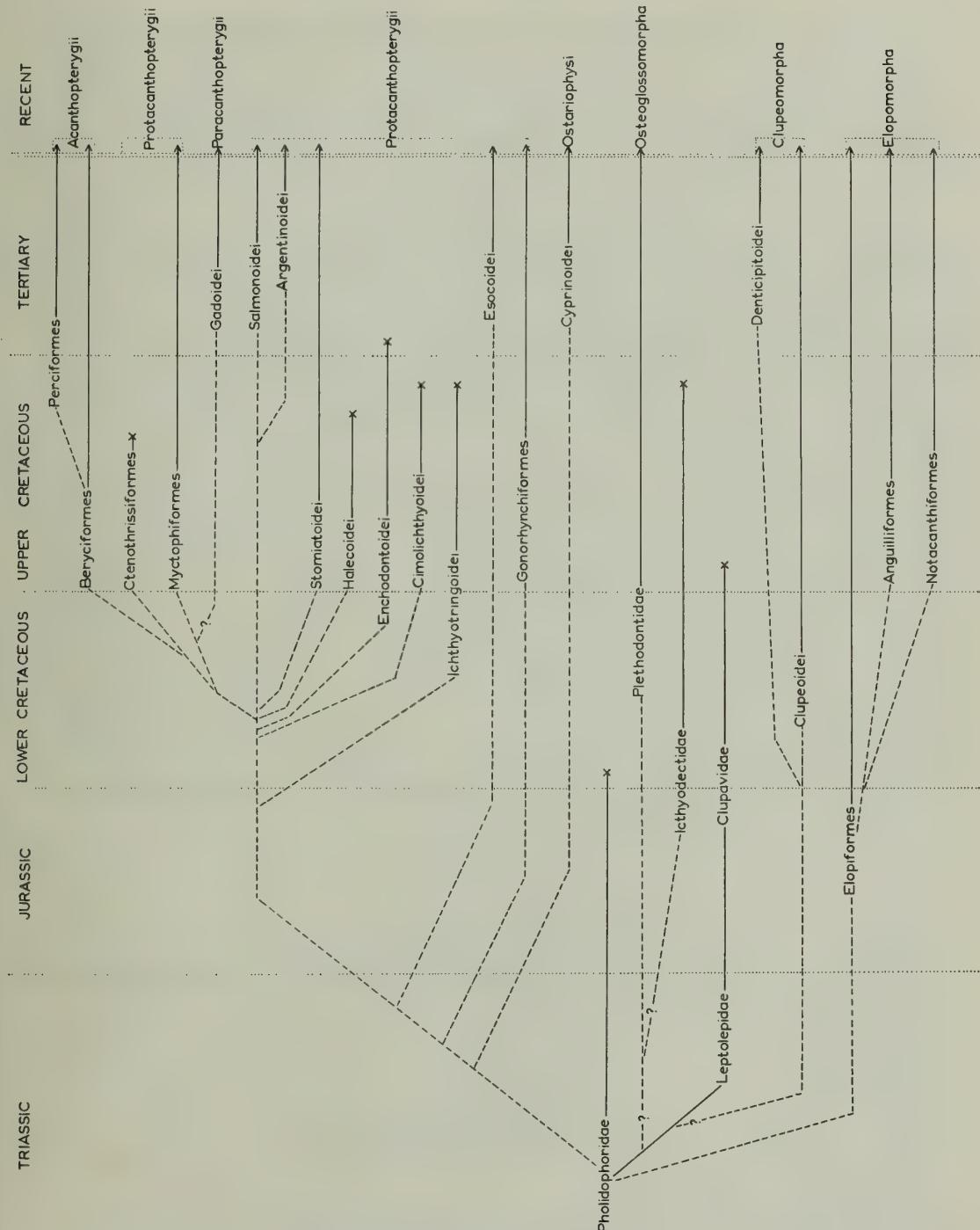


FIG. 102. Evolutionary tree of the Teleostei from the Triassic to the present day.

the origin of a considerable proportion of the recent bathypelagic fauna is accounted for when viewed in the light of the competition for food and living space with the Acanthopterygii.

The evolutionary considerations outlined in the present section are summarized in Text-figure 102.

V. CONCLUSIONS

In the foregoing descriptions and discussion some mention has been made of the divergence between on the one hand the Elopomorpha and on the other the salmoniform group and its derivatives. The Elopiformes have been considered in the last section to be very close to the halecostomes, with the Elopoidei retaining the greatest number of halecostome characters (Nybelin, 1956). Certain specializations, however, rule this group out from the main course of teleost evolution (Greenwood, *et al.*, 1966 : 348). The Salmoniformes do not possess any of the limitations of the elopiforms and it has been shown that the major teleost radiations had their origin within the Salmoniformes.

The reality of the divergence between the Elopiformes and the Salmoniformes has been indicated but this divergence may in part be due to the absence of fossil salmoniforms in deposits earlier than the Albian. The elopiform lineage is distinct by the Upper Jurassic and undoubtedly arose somewhat earlier. The salmoniforms, first represented in the marine Albian, may have also been present in the Jurassic, but in fresh water. If this is the case then the basal members of the two groups would possibly have shown a much closer resemblance. The Ichthyotringoidei has been proposed as being the most primitive of the Cretaceous salmoniforms so far described and certain osteological features, notably the caudal skeleton, are as easily comparable with an elopiform as with a salmoniform. Although the two lineages might approach one another more closely basally, both probably having been derived from the Pholidophoridae, there appears to have been a marked divergence in evolutionary potential between the two groups.

The structure of the jaws has been stressed as being one of the major factors influencing the course of later teleost evolution. In the Elopomorpha the jaw is non-protrusile and there is no mechanism enabling the premaxilla to be moved forwards, while the maxillae form the majority of the upper jaw margin. The salmoniform derivatives on the other hand exhibit protrusibility of several types, the essential factor being that the jaw is capable of becoming protrusile. Eaton (1935 : 168) and Alexander (1966 ; 1967a ; 1967b : 250) have outlined three main types of jaw protrusion, an ostariophysan type, a cyprinodont type and a true acanthopterygian type. Eaton goes on to say that these three types possess an enlarged premaxilla with a median dorsal process which suggests a common origin. Considering the comments of Allis (1909), Greenwood, *et al.* (1966), Weitzman (1967) and Goody (1968) it is possible that the dorsal processes are homologous and the three types share a common ancestry.

Supporting evidence for the closeness of the basal stocks of the Salmoniformes, Myctophiformes, Ctenothrissiformes and Beryciformes is afforded by the structure

of the caudal skeleton. This complex is remarkably similar in all four groups and undergoes identical fusions and reductions.

Other trends exhibited by the salmoniform derivatives also separate them from the elopiforms, for example the constellation of characters associated with the paired fins and increased manoeuvrability. However fin spines are produced in the more specialized derivatives of both lineages (Marshall, 1962, has demonstrated the presence of true fin spines in the *Heteromi*) being due to the stresses imposed on the fins by increased momentum and bodily flexion (Patterson, 1964).

Thus after the separation of the elopiform and salmoniform lineages at the level of the pholidophorid halecostomes the salmoniforms appear to have evolved possibly in fresh water for some considerable time. During this period many changes were effected within the Salmoniformes. Their subsequent radiation back into marine environments in the Lower Cretaceous involved much 'experimentation', both successful and unsuccessful, in respect of survival to the present day. These evolutionary 'experiments' have all been along somewhat similar lines with the same changes and deletions occurring time and again. These changes have been manifested in all parts of the skeleton, the skull, vertebral column, paired fins and girdles, and lastly in the caudal skeleton. However the majority of groups have also exhibited changes and specializations peculiar to themselves as well as showing the general trends present in all of the groups. Thus a variety of radiations occurred into particular ecological niches. Certain of these radiations are represented by the salmoniform suborders Cimolichthyoidei, Enchodontoidei and Halecoidei. In many groups the specialization for a particular mode of life has proceeded to such an extent that often any evolutionary plasticity exhibited by the parent stock is lost. Whilst filling their ecological niche successfully (success being based on their relative abundance in the fossil record) these forms seem to have been adversely affected by competition from later radiations. These later forms have advanced to a greater degree of efficiency in many aspects of life but still seem to have retained a more generalized overall construction and are still capable of further variability. This competitive aspect presumably accounted for much of the extinction of groups successful through the Upper Cretaceous.

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VIII. LETTERING USED IN THE TEXT-FIGURES

a.e.pal	anterior extent of the palatines	c	centrum
a.e.pm	anterior extent of the premaxillae	ch	ceratohyal
ang	angular	cl	cleithrum
ant	antorbital	cor	coracoid
ar.p.pm	articular process of the maxilla	c.pt.f	interspace of cartilage in the floor of the post-temporal fossa
art	articular		
art.f	articular flange lateral to the articular facet	den	dentary
as.p.pm	ascending process of the premaxilla	den.t	anterior, enlarged dentary tooth
a.t.f.c.	anterior opening of the pars jugularis	d.f	dilatator fossa
		d.pcl	dorsal postcleithrum
b.f	basal fulcral scale	d.pt	dorsal limb of the post- temporal
b.md.V	foramen of branch of mandibu- lar (trigeminal) nerve		
bo	basioccipital	ecp	ectopterygoid
brs	branchiostegal rays	ecp.t	ectopterygoid tooth
bs	basisphenoid	enp	endopterygoid
		enp.t	endopterygoid teeth

ep 1		la	lachrymal
ep 2	1st, 2nd and 3rd epural bones	l.e	lateral ethmoid
ep 3		l.l	course of the lateral line
epo	epiotic		sensory canal
exo	exoccipital	l.l.sc	lateral line scale
f.art	articular facet	m.cor	mesocoracoid arch
f.e.p.a.	foramen of the efferent pseudobranchial artery	med.s.c	sensory canal in the mid-dorsal line
f.f	facial foramen	mes	mesethmoid
f.hm	articular facet for the hyomandibular	mpt	metapterygoid
f.i.c.a.	foramen of the internal carotid artery	mx	maxilla
f.l.e	facet for the lateral ethmoid	mx.g	maxillary groove on the palatine
f.m	foramen magnum	mx.p.p	maxillary process of the palatine
f.mes.vo	facet for the mesethmoid and vomer	myo	myodome
f.o.n	foramen for occipital nerve	n.a	neural arch
f.o.a	foramen for orbital artery	na	nasal
f.p	facet for palatine	na.pu 1	neural arch of the first preural vertebra
f.d.pt	facet for the dorsal limb of the post-temporal	na.pu 2	neural arch of the second preural vertebra
f.v.pt	facet for the ventral limb of the post-temporal	na.u 1	neural arch of the first ural vertebra
fr	frontal	n.s	neural spine
f 1. ecp	facets for the articulation of the palatine with the ectopterygoid	o.inf.s.c	otic branch of the infraorbital sensory canal
f 2. ecp		op	operculum
g.md. VII	groove for the mandibular branch of the facial nerve	op. VII	foramen of the opercular branch of the facial nerve
g.sym	symplectic groove of the quadrate	op.p.hm	opercular process of the hyomandibular
h.a	haemal arch	ors	orbitosphenoid
hh	hypohyal	ot. VII	foramen of the otic branch of the facial nerve
hm	hyomandibular	p. VII	course of the palatine branch of the facial nerve
hm.h	head of the hyomandibular	pa	parietal
hm. VII	foramen of the hyomandibular nerve within the hyomandi- bular bone	pal	palatine
h.mx	articular head of the maxilla	pal.t	palatine tooth
h.s	haemal spine	par	parasphenoid
hy	hypural (numbered 1-6)	pcl	postcleithrum
ic	intercalar	p.e.f	fenestra entering the cranial cavity below the post- temporal fossa
inf	infraorbital bone (numbered 1-6)	p.f	profundus foramen
inf.s.c	infraorbital sensory canal	ph	parhypural
iop	interoperculum	p.ecp	palatine prominence for articulation with the ectopterygoid

pls	pleurosphenoid	so.s.c	supraorbital sensory canal
pm	premaxilla	so. V, VII	foramen of the superficial ophthalmic nerves
pm.f	fenestra in the ascending process of the premaxilla	soc	supraoccipital
pop	preoperculum	sop	suboperculum
pop.s	preopercular spine	spo	sphenotic
post.z	postzygapophysis	s.pop	suprapreoperculum
pop.s.c	preopercular sensory canal	st	supratemporal
prez	prezygapophysis	st.s.c	supratemporal sensory canal
pro	prootic	su	stegural
pro.b	prootic bridge	sym	symplectic
pt	post-temporal	t.f	trigeminal foramen
pt.f	post-temporal fossa	t.ps	transverse process
p.t.f.c.	posterior opening of the pars jugularis	u 1 } u 2 }	ural vertebrae one and two
pto	pterotic	ur 1 } ur 2 }	uroneurals one and two
pu	preural vertebra (numbered 1-9)	vo	vomer
pu 1 + u 1	preural vertebra one fused with ural vertebra one	vo.t	vomerine teeth
p.vo	prominence for articulation with the vomer	vpcl	ventral postcleithrum
q	quadrate	v.pt	ventral limb of the post-temporal
r.n.s.pu 2	reduced neural spine of the 2nd preural vertebra	III	foramen of the oculomotor nerve
s.c	foramen of sensory canal	VII.hm	foramen of the hyomandibular nerve in the prootic
sca	scapula	VII.p	foramen for the palatine branch of the facial nerve
sca.cor	scapulocoracoid	IX	foramen of the glossopharyngeal nerve
sca.for	scapular foramen	X	foramen of the vagus nerve
scl	supracleithrum		
smx	supramaxilla		
smx 1	anterior supramaxilla		
smx 2	posterior supramaxilla		
so	supraorbital		



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